Comparative flowering ecology

of *Fraxinus excelsior*, *Acer platanoides*, *Acer pseudoplatanus* and *Tilia cordata*

in the canopy of Leipzig's floodplain forest

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Abstract

How do gender separation and the transition to wind pollination happen in temperate trees? What does the reproductive ecology in the crowns of temperate forest trees look like? These connected questions intrigued researchers before and since Darwin but it is only in the last years that a direct study of the latter question has been enabled. A research crane was used to study the flowering ecology of *Fraxinus excelsior*, *Acer platanoides*, *Acer pseudoplatanus* and *Tilia cordata* in Leipzig's floodplain forest. These species originate from hermaphrodite insect pollinated plant families and exhibit different grades of gender separation and different stages between insect and wind pollination. As they are typical elements of temperate deciduous forests, an ecological comparison of their flowering ecology may shed new light on the evolution of gender separation and wind pollination in this habitat. Using the crane, gender distribution, flowering phenology in relation to microclimate, pollination levels (including pollen tubes in the styles) and fruit set were studied in ca. 200 trees over 2-4 years. Main results are a new appreciation of the sexual system of *Fraxinus excelsior* as dioecy, of *Tilia cordata* as andromonoecy and a detailed description of the intricacies of the heterodichogamous sexual system of *Acer pseudoplatanus*. Several flowering phenological patterns are described in *Fraxinus excelsior* and *Acer platanoides* in relation to microclimate in early spring. The role of small arthropods is underlined as gall mites may play a role in gender specialisation in *Fraxinus excelsior*, gall midges are related to maleness in *T. cordata* and thrips are probably the pollinators of *Acer pseudoplatanus* in the stand. Thrips pollination is suggested to be a possible stepping-stone between insect pollination and wind pollination, which may drive the transition in *Acer pseudoplatanus* and possibly in intensively flowering dominant species in other habitats. The study presents the complexity of the reproductive systems and the strong interdependencies among their elements.

Contents

Introduction

This study is an attempt to approach an old problem with a new means. The problem is how do gender separation and wind pollination evolve in temperate trees from hermaphrodite insect pollinated ancestors and the new means is a research crane, enabling easy access to the canopy of a mature forest stand.

Fraxinus excelsior, *Acer platanoides*, *Acer pseudoplatanus* and *Tilia cordata* present different grades of gender separation and of tendency to wind pollination, yet they origin from mostly hermaphrodite and insect pollinated families. These species are typical to deciduous forests in continental and geological scales, so that their evolution could have occurred under the influence of similar ecological factors. An ecological comparison of their reproductive biology may thus through new light on this problem.

Canopy access enabled a unique study of reproductive biology, from gender distribution through flowering phenology and pollination to fruit production, of many large individual trees, so that the species could be compared from many facets. The floral biology of these species has not yet been studied directly in the crowns of mature trees.

The introduction begins with a brief background on gender separation and pollination modes presenting the "old problem", its current solutions and their insufficiencies, continues with the position of flowering phenology as a central reproductive process, and then turns to describe deciduous forests and the studied species.

Gender separation

Flowering plants present a wide range of sexual systems (Lovett Doust 1990, Richards 1997), reflecting their modularity and phenotypic plasticity (Silvertown and Gordon 1989, Wayne and Bazzaz 1991). Hermaphroditism is the rule, but about a quarter of the species show gender separation to different degrees (Yampolsky and Yampolsky 1922, Richards 1997).

Definitions of gender are applied at the levels of the flower, the inflorescence, the plant, the population and the species. The following definitions follow Sakai and Weller (1999) and Richards (1997):

1. A flower with both female and male parts (pistil and stamens respectively) is called hermaphrodite (also perfect or monoclinous), a flower with one functional gender is called pistilate or staminate. The inflorescence may be composed of flowers of one type or may include flowers of different genders.
2. A plant with all flowers of one type is called hermaphrodite (H), female (F) or male (M) respectively **(**rounded parentheses are used here to denote variation within a plant**)**.
3. In plant populations or species, both levels of the plant and the group of plants may vary **[**rectangular parentheses denote the range of plant forms in the population**]**:
    a. Monomorphic populations include plants with the same gender expression, e.g. hermaphrodite (also homoecious, Cruden and Lloyd 1995): [(H)], monoecious: [(F,M)], andromonoecious: [(H,M)], gynomonoecious: [(H,F)].
    b. Dimorphic populations include plants differing in gender expression, e.g. dioecious: [(M),(F)], androdioecious: [(H),(M)] and [(F,M),(M)], gynodioecious: [(H),(F)].
    c. Polymorphic populations may exhibit a large diversity of sexual types (Schultz 1892, Yampolsky and Yampolsky 1922). Two generic terms are subdioecy: [(F),(M),(M with some H)] and polygamy: [not fitting into any other term] (Sakai and Weller 1999).

These definitions are usually applied by evaluating the floral morphology. Plant gender may be defined from a functional point of view as well (Lloyd 1980), i.e. whether its main contribution to seed production is through paternal (pollen) or maternal (ovules) routes (male and female respectively) or through both routes (hermaphrodite). The definitions for the gender types stay the same as above, but obtain a different meaning (Lloyd and Bawa 1984). The quantification of paternal and maternal contributions is methodologically difficult and requires much abstraction (Lloyd 1980), but brings about a functional appreciation of intermediate states, and usually a simplification of definition – systems that seemed complicated are unveiled as basically simple (e.g. Webb 1979, Primack and McCall 1986, Mayer and Charlesworth 1991, Verdú, Montilla and Pannell 2004).

Plants may change gender during life (Lloyd and Bawa 1984). Changes are categorised as either gender switching or gender adjustment, the latter being smaller and much more widespread among plant species (Freeman et al. 1980, Policansky 1982, Lloyd and Bawa 1984, Cox 1990, Schlessman 1990). Many factors may affect gender expression in plants, e.g. abiotic factors like nutrient and water availability and climate, and intrinsic and extrinsic biotic factors (e.g. plant age, genetic regulation or herbivores, from deer to eriophyoid mites - Chailakyan 1979, Malik and Bhattacharya 1979, Freeman et al.1980, Meagher 1990, Richards 1997, Årgen et al. 1999, Fritz et al. 2003).

Dichogamy, the temporal separation of gender on a plant during a flowering season, is common among flowering plants (Richards 1997) and may take the forms: Protogyny (female expression first), protandry (male expression first) and heterodichogamy (protogynous, protandrous and possibly other individuals, Stout 1928, de Jong 1976 and 1994, Gleeson 1982, Dommée et al. 1995, Pendleton et al. 2000), which is considered the temporal analogue to heterostyly (Müller 1875, Darwin 1877, Cruden 1988, Renner 2001, Barrett 2002).

Hermaphrodite dominance in flowering plants is explained by the advantage of resource sharing (e.g. attractive structures, pollen as food) by male and female functions to attract biotic pollinators (Charnov et al. 1976). A second advantage may be the possibility to sire offspring at low density of co-species or pollinators, given compatibility (Pannell 2002).

Separation of gender is considered to enable:

1. Independent specialisation in male and female function (Freeman et al. 1976, Givnish 1982, Bierzychudek and Eckhart 1988, Meagher 1990, Ashman 2002, but see Bawa and Opler 1977, Willson 1986). Understanding of the reproductive aspects of the specialisation is helped by assessing or modelling the allocation of plant resources to male and female function (Charnov et al. 1976, Charnov 1982, Lovett Doust and Lovett Doust 1990, Charlesworth and Morgan 1991, Brunet 1992, Campbell 2000) and by discussing different reproductive strategies of male and female gender (Sutherland and Delph 1984, Burd and Head 1992, Crawley 1997a).
2. Reduction of the interference of self-pollen, both in fertilisation (Charlesworth and Charlesworth 1978, Baker 1984, de Jong et al. 1992, Traveset 1999) and in pollination process (stigma clogging, Bawa and Beach 1981, pollen discounting, Harder and Willson 1998). This aspect includes the regulation of selfing and outcrossing (Jarne

1993, Richards 1997 but see Bertin 1993) and avoidance of inbreeding depression (Charlesworth and Charlesworth 1978, Ross 1980).

The grade to which these functions are active depends on the level of gender separation, e.g. in monoecious species generative specialisation is possible and some reduction of selfing, whereas in dioecious species also vegetative specialisation (and a total reduction of selfing) may be achieved (Delph 1999, Årgen et al. 1999).

Different types of gender separation are ordered along "pathways" leading from hermaphroditism to dioecy (Ross 1982, Webb 1999). The two central pathways are over gynodioecy and over monoecy (Barrett 2002). This study deals with two rare and poorly understood pathways (Charlesworth 1984, Renner 2001):

1. Over andromonoecy and androdioecy (Ogata 1967 in *Acer,* Wallander 2001 in *Fraxinus* over androdioecy only). Andromonoecy is interpreted as enabling the production of pollen excess under a given limitation of ovule or fruit production (e.g. Primack and Lloyd 1980 in *Leptospermum*, Diggle 1988, Connolly and Anderson 2003 and Miller and Diggle 2003 in *Solanum*, Cuevas and Polito 2004 in *Olea,* Ito and Kikuzawa 1999 in *Tilia japonica*), whereas androdioecy is considered to be derived from dioecy and to enable reproduction by selfing in low density populations (Rieseberg et al. 1992 in Datiscaceae, Akimoto et al. 1999 in *Schizopepon*, see Barrett 2002 and Pannell 2002 for review).
2. Over heterodichogamy (suggested for the genus *Acer*, de Jong 1976, Webb 1999, Verdú and Gleiser 2006). Heterodichogamy already includes different types, and it is suggested that further gender specialisation of these types may lead to dioecy (Gleeson 1982, McCarthy and Quinn 1990 and Kimura et al. 2003 in Juglandaceae, Dommée et al. 1990 and 1995, Ramadan et al. 1994 and El-Kebawy et al. 1996 in *Thymelaea hirsuta* in which protandrous plants were more female, and Pendleton et al. 1988 and 2000 in *Grayia brandegei*, in which protogynous plants were more female).

Separation of gender is to some extent history bound, as both phylogenetical and geographical correlations to its appearance are found. Renner and Ricklefs 1995 report "phylogenetic environments" with tendency to gender separation (see also Weller and Sakai 1999) and gender separation increases northwards in trees with small flowers (Fox 1985). The plant characters, which are most strongly correlated with gender separation, are (Vamosi et al. 2003):

1. Abiotic pollination (Fox 1985, Renner and Ricklefs 1995).
2. Fleshy fruit (Bawa and Opler 1975, Givnish 1982).
3. Small inconspicuous flowers (Givnish 1982, Muenchow 1987).
4. Woody habit (Thompson 1986) and climbing habit (Renner and Ricklefs 1995).

Gender separation, especially monoecy and dioecy, are frequently found in temperate latitudes and especially in trees.

This study of gender separation points at the less studied aspects:

1. A comparison of unrelated species with different grades of gender separation, which grow under similar ecological circumstances that commonly lead to gender separation.
2. Gender separation as part of the whole reproductive ecology of the studied trees.
3. A first canopy study of gender separation in *Fraxinus* and *Acer* in mature trees in a semi-natural stand. The genera represent the rare pathways androdioecy and heterodichogamy (respectively).

Pollination modes

Specialised pollination modes are commonly ascribed pollination syndromes that usually include flowers with complex morphology and animal pollinators (Faegri and van der Pijl 1966, Kugler 1970, Kevan and Baker 1983 and 1999, Proctor et al. 1996, Howe and Westley 1997, Richards 1997, Armbruster et al. 2000, Leins 2000, Fenster et al. 2004). Wind pollination, anemophily, is the commonest abiotic pollination syndrome (Ackerman and Kevan 2005), and refers to a suit of floral morphological and phenological adaptations. These include:

1. Release and capture of pollen by aerodynamically specialised structures (e.g. cones, catkins, pendulous inflorescences, Faegri and van der Pijl 1966, Niklas 1985, Crane 1986).
2. Flowers consist mainly of stamens and pistils that are commonly separated between different flowers (i.e. monoecy or dioecy, Ackerman 2000, Leins 2000).
3. Pistils include one or very few ovules (Pohl 1930, Wagenitz 1975, Burd 1995) and sometimes feathery stigmas (Kevan 2005).
4. Powdery pollen between 20-40µ (Whitehead 1969, upper limit 60µ in Niklas 1985), that is produced in a large amount (Crudan 2000). The pollen grains are scantly

sculptured but have a specialised morphological functionality (Hesse 1981, Crane 1986).

Climatic and structural parameters play an important role in determining the distribution and flowering time of anemophilous plants – they usually grow close together in regions with a leafless and/or dry and/or windy season, where there are clear climatic cues to flowering (Whitehead 1969 and 1983, Kugler 1971, Regal 1982, Dafni 1992, Kevan 2005).

Generalised insect pollination (referred to as entomophily in the following) typically involves small inconspicuous flowers and different insects (Proctor 1978, Waser et al. 1996). It is considered ancestral in angiosperms (e.g. Linder 1998 but see Meeuse 1989), is common (Proctor 1978, O'Brien 1980, Williams and Adam 1999, Thompson 2005) and gains increasing attention of pollination biologists (Heinrich 1975, O'Brien 1980, Waser et al. 1996, Herrera 1996, Johnson and Steiner 2000, Olesen 2000, Smith-Ramírez et al. 2005). The borders between this "syndrome" and specialised syndromes is often not clear, as systems considered specialised by flower morphology are sometimes found to be generalised when quantifying the contribution of different visitors to pollination (O'Brien 1980, Armbruster et al. 2000), and systems considered generalised by flower morphology are sometimes found to be effectively pollinated by few or one of its diverse visitors only (Bawa 1990, Dafni 1992, Kearns and Inouye 1993, Howe and Westley 1997, Gross 2005, Potts 2005), which means that they are actually specialised. Brood-site or nursery pollination (Sakai 2002, Dufaÿ and Anstett 2003), in which the pollinator reproduces in the flowers or fruit, may also be mistaken for a generalised pollination if the flowers do not have an exceptional morphology.

Small and inconspicuous insects are sometimes found to be specialised pollinators of seemingly generalised flowers (e.g. Sowter 1949, *Theobroma cacao* in Free 1970, Vogel 1978, Webber and Gottsberger 1995, Gottsberger 1999, Sakai et al. 2000, Goldblatt et al. 2004 and see below). Their size, behaviour and difficulty to exclude render such insects to be overseen or ignored in the analysis of pollination systems. Thrips (Thysanoptera) are notoriously inexcludable small flower visitors (Müller 1873, Darwin 1876 and 1877, Kirk 1997), that were actually found to be the main pollinators of diverse plant groups such as:

1. Large forest trees such as dipterocarps (Kavanagh 1979, Ashton et al. 1988), anonaceen (Webber and Gottsberger 1995, Momose et al. 1998, Gottsberger 1999), moraceae (Sakai 2001, Zerega et al. 2004), *Macaranga* spp. (Moog 2002, Moog et al.

2002), *Jatropha curcas* (Solomon Raju and Ezradanam 2002), and mahagony (after Kirk 1997).

2. Several primitive angiosperms (Bernhardt and Thien 1987, Gottsberger 1988 and 1999, Pellmyr et al. 1990, Lloyd and Wells 1992), and also cicads (Mound and Terry 2001). These lead Terry (2002) to suggest thrips as the "primeval pollinators".
3. Shrubs like *Lantana camara* (Mathur and Mohan Ram 1986), *Calluna* and *Erica* (Hagerup 1950 and 1951, Hagerup and Hagerup 1953 but see Haselrud 1974, Mahy et al. 1998) and the heterodichogamous *Thymelaea hirsuta* (Cornara et al. 2005).
4. Herbs like *Ranunculus* and *Potentilla* (Baker and Cruden 1991), Brassicacea (Gómez and Zamora 1996), Asteraceae (Ananthakrishnan and Gopinathan 1998) and different crops (Free 1970, Kirk 1997).

Kirk (1997) suggests a thrips pollination syndrome and discusses its possible importance.

Ambophily, co-occurring insect and wind pollination, is discussed for many species with small flowers (e.g. Dafni and Dukas 1986, Linder 1998, Goodwillie 1999, Williams and Adam 1999, Culley et al. 2002, Cresswell et al. 2004). It is considered the intermediate state in the transition from (generalised) entomophily to anemophily, that has occurred many times independently (Cox 1991, Tisch and Kelly 1998, Culley et al. 2002, Ackerman and Kevan 2005). The transition itself is accredited to an increasing efficiency of anemophily, e.g. due to limitations of pollinators (Vroege and Stelleman 1990, Cox 1991, Linder 1998, but see Regal 1982). Ambophily was intensively studied in *Salix*, in the context of its possible return from anemophily to entomophily (Meeuse 1978, Stelleman 1984, Vroege and Stelleman 1990, Tollsten and Knudsen 1992, Tamura and Kudo 2000) and in *Plantago*, in relation to its breeding system (Primack 1978, Stelleman 1978, Sharma et al. 1992). Other species and genera were studied in the current context of the change from insect to wind pollination, for example *Cocos nucifera* (Meléndez-Ramírez et al. 2004), *Buxus balearica* (Lázaro and Traveset 2005), *Calluna* (and *Erica tetralix*, Hagerup 1950 and 1951, Hagerup and Hagerup 1953, Haselrud 1974, Mahy et al. 1998), *Shorea* (Atluri et al. 2004) and *Espeletia* (Berry and Calvo 1989, Monasterio and Sarmiento 1991). The latter three genera present geographical differences in the effective pollinator - at least in *Calluna* and *Shorea* thrips are sometimes effective pollinators and *Espeletia* presents an increasing reliance on wind pollination with the elevation in the Andes, accompanied with changes to nodding inflorescences (capitulae) and a larger flower number as response to lower pollinator numbers (but see caveats in Arroyo et al. 1985). The genera *Fraxinus*, *Acer* and *Tilia* were studied in this respect using intrageneric

comparisons (e.g. Ogata 1967, Hesse 1978 and 1979a-c, Paw U and Hotton 1989, Wallander 2001, Grimm 2005). Ecological studies of *A. pseudoplatanus* and *T. cordata* resulted in different importance of insects (bees and flies) and wind for their pollination (see details below).

Wind pollination is assumed to promote gender separation by relieving the limitations imposed by insect pollination (Charnov et al. 1976, Charlesworth 1993), by enhancing the possibilities of sexual specialisation (male fitness increases linearly with plant size whereas female fitness saturates, Charnov 1982, Schoen and Stewart 1986, but see Charlesworth and Morgan 1991) especially in large plants (Wallander 2001 for *Fraxinus*), and by the avoidance of selfing (Culley et al. 2002, however Kaplan and Mulcahy 1971 suggest that avoidance of selfing promoted dicliny, and that dicliny promoted anemophily in the originally entomophilous *Thalictrum*). Linder (1998), relying on a phylogentical analysis, proposes that many of the differences between anemophilous and entomophilous species (e.g. gender separation) actually evolved after the transition to anemophily from ambophilous predecessors had occurred. He leaves dichogamy, small flowers and more or less dry pollen as sole prerequisites to an evolution of anemophily.

The pollination mode affects the patterns of pollen flow and fruit production in the plants (Culley et al. 2002). Dispersal of pollen by wind is governed by different parameters than dispersal of pollen by insects (Burrows 1975a, Frankie et al. 1983, Niklas 1985 and 1988, Crane 1986, Bolick 1990, Kevan 1990, Chittka et al.1997,) and result in a different mating pattern in the population (degree of selfing and effective population size Crawley 1997a). See further introduction below.

Two difficulties in this “twilight zone” between entomophily and anemophily are:

1. A large reduction in the efficiency of entomophily is needed before anemophily becomes efficient. This is because these pollination modes present opposite requirements from several floral traits such sticky versus powdery pollen, attractive structures and monocliny versus reduction of distractions and dicliny (respectively), and potentially different requirements from other floral traits e.g. flowering time, type of dichogamy, amount of pollen and stigma structure (Hesse 1981, Bollick 1990, Karrenberg et al. 2002, Sargent and Otto 2004).

2. Small insects are usually ignored when studying ambophily (Cox 1991, Culley et al. 2002). This conceptual lack is most obvious on the applied methodology, using nets of ca. 1mm mesh size to exclude insects (Vroege and Stelleman 1990, Binggeli 1992, Mahy et al. 1998, Karrenberg 2002, Meléndez-Ramírez et al. 2004, Lázaro and Traveset 2005, exceptions are Baker and Cruden 1991, Moog 2002 and Moog et al. 2002, and partly the use of slides within the covers, e.g. Dafni and Dukas 1986, and the direct study of efficiency of wind polliantion, e.g. Cresswell et al. 2004). This mesh size hardly affects small insects such as thrips, that are renown for their ability to get into any cover (Müller 1873, Darwin 1877, Kearns and Inouye 1993, Kirk 1997). The technical difficulty is fundamental, as smaller mesh sizes also impede wind pollination and commonly affect strongly the microclimate around the flowers, which may change the floral biology (Dafni 1992).

Flowering phenology and pollen exchange in the population

Phenology is the study of timing in life history (Lechowicz 2001). The timing of flowering is a basic reproductive parameter, as it determines the chances of a plant to donate and receive pollen (Primack 1985, Crawley 1997a, Fox 2003). Flowering phenology is a central process connecting the sexual system and pollination mode of the plant with its actual pollination and fruit and seed production (Lindsey 1982, Zimmerman 1984, Rathcke and Lacey 1985, Primack and Kang 1989, Barrett and Eckert 1990). It affects the variability in the offspring population and is itself affected by this resulting variability (Schmitt 1983, Primack 1985, Dieringer 1991, Pigliucci 1996).

Flowering phenology affects also organisms that interact with the plants, such as florivores (flower exploiters), frugivores (fruit eaters) or other herbivores (Brody 1997, Leather 2000, Wright and Meagher 2003) as well as pollinators. Changes in phenology may result in a feedback on plant reproduction as well as in effects on large parts of the ecosystem (especially in trees, Stenseth and Mysterud 2002). Practically, understanding the timing of flowering may be used to predict allergy risk and the timing of agricultural actions (Chmielewski 2003).

Flowering phenology may be studied at different levels from the single flower through the single plant and the whole population and up to a species or a flora (Primack 1985). Flowering phenology of trees has mostly been studied in the tropics in the context of flowering patterns over the years and the description of phenology within the crown usually

includes flowering intensity only (Bawa 1983, Rathcke and Lacey 1985, van Shaik et al. 1993, Newstrom et al. 1994, Wesenberg 2004). Temperate trees usually flower annually because of the limited vegetation period, but may present supra annual patterns. Mast behaviour is fruit production in a supra annual, commonly biannual rhythm (Crawley 1997b, Kelly and Sork 2002). This behaviour was related to many different, not mutually exclusive factors, such as weather conditions and cues (Kelly and Sork 2002), predator satiation (Janzen 1971, Tapper 1992a, Kelly and Sork 2002, Kon et al. 2005), resource availability (Sork et al. 1993, Miyazaki et al. 2002), explicitly mycorrhiza (Newbery 2005), wind pollination (Tisch and Kelly 1998, Smith et al. 1990), fruit size (Ostfeld and Keesing (2000), natural selection of seedlings (Taylor and Aarssen 1989), and synchronisation of flowering phenology (Lalonde and Roitberg 1992, Tapper 1992a), as well as combination of several factors (Smith et al. 1990, Sork et al. 1993, Herrera et al. 1998, Houle 1999).

Patterns within the crown may be interesting to study, as microclimatic differences within the crown are potentially larger than in the tropics due to stronger daily and seasonal fluctuations. Macroclimate and its annual variation as well as microclimate have a large effect on flowering (Jackson 1966, Stoutjesdijk and Barkman 1992, Lechowicz 1995) as floral development depends in many of its steps on different climatic parameters (Taiz and Zeiger 2000, Henderson et al. 2003, Komeda 2004, Körner in press). Warming up from winter to spring occurs in an irregular way and the climatic variation is pronounced. Indeed early spring flowering phenology is one of the most sensitive biological processes that are used to indicate climate change (Schwartz 1999, Chiemelevsky and Rötzer 2000, Sparks 2000, Menzel et al. 2001, Fitter and Fitter 2002, White et al. 2003).

Temporal gender separation at flower level may or may not be synchronised in the whole plant. Thus dichogamy at flower level may be reinforced but may also be countered by the temporal pattern of flowering in the whole plant. Monoecious systems, for example, may be functionally hermaphrodite if male and female gender are expressed synchronously, or temporally dioecious if they are asynchronous (Cruden and Hermann-Parker 1977, Cruden 1988). Synchronisation at plant and stand level is an important characteristic of flowering phenology and is intimately connected with the sexual system and pollination mode of a plant species (Primack and Lloyd 1980, Augspurger 1981 and 1983, Primack 1985, Bolmgren 1998, Albert et al. 2001) and together with the locations of the individual trees determines their reproductive chances and mates (Zimmerman and Gross 1984, Primack 1985, Barrett

and Eckert 1990, Dieringer 1991, Fox 2003, but see also Ollerton and Lack 1992, Albert et al. 2001). Pollination of a plant that flowers asynchronous from the rest of the population can be selfing at most and a population with a low flowering synchrony may have a lower reproductive success, a lower outcrossing rate and a lower variety of pollen sources and acceptors than in a population in which flowering is synchronous at stand level (Augspurger 1981, Smith et al. 1990, Brody 1997, Fromm 2001, Fox 2003).

Selfing may assure pollination success (Richards 2003), but outcrossing results in a higher variability of offspring (Campbell 1985, Charlesworth and Charlesworth 1995, Delph et al. 1997). Different pre- and post-pollination mechanisms (Willson and Burley 1983, Richards 1997) act against selfing, such as gender separation, incompatibility (Barrett 1990, De Nettancourt 2000, Franklin-Tong and Franklin 2003, Hiscock and Tabah 2003) and inbreeding depression (Darwin 1876, Jain 1976, Charlesworth and Charlesworth 1987, Carr and Dudash 2003). Plants range the whole spectrum between fully selfing (at least almost, Richards 2003) and fully outcrossing (Kearns and Inouye 1993, Traveset 1999, Barrett 2003), depending on their ecology and dispersal opportunities (Jain 1976, Jarne and Charlesworth 1993, Richards 1997).

Geitonogamy, selfing between different flowers on one plant, is especially likely in large plants such as trees that are mass flowering, and its avoidance in them requires strict temporal or spatial separation of genders and a synchrony of flowering at the tree level (Arroyo 1976, Stephenson 1982, de Jong et al. 1992, Barrett and Harder 1996, Snow et al. 1996, Spira et al. 1996). Even in self-incompatible plants, high self-pollen loads disturb the pollination process through pollen discounting and stigma clogging (Brunet 2005).

The efficiency of pollination includes the processes of pollen transport (Pacini 1992) and fertilization of the ovules till the production of viable seeds (Cresti et al. 1992, Inouye et al. 1994). The pollination mode is responsible for the first part of this process, whereas male competition during the growth of pollen tubes and female selection at this stage and afterwards are responsible for its second part (Willson and Burley 1983, Mulcahy and Mulcahy 1987, Lee 1990, Mascarenhas 1990, Walsh and Charlesworth 1992, Snow 1994, Willson 1994, Delph et al. 1997, Burd 1998, Pasonen et al. 1999, Erbar 2003, Stephenson et al. 2003).

The pollen load set by the pollination vector affects the intensity of pollen tube competition among male gametophytes (Cruden and Miller-Ward 1981, Stone et al. 1995, Niesenbaum 1999, Edlund et al. 2004), as well the probability for fertilization and complete development of a seed (i.e. its chances not to be aborted, Stephenson 1982, Bawa and Webb 1984, Sato 2000) and also the genetic quality of the seed (Ellstrand 2003, Charlesworth and Charlesworth 1995, Primack and Kang 1989, Campbell 1985). The level of natural pollen tube competition is necessary to assess the importance of this process, but was studied only in a few plants (Honig et al. 1992, Herrera 2002 and references therein) and as far as I know in no tree species. Studies of pollen loads show that bees deposit many pollen grains (tens to hundreds, e.g. Silander and Primack 1978, Thomson and Plowright 1980, Erbar 2003) but natural pollination level is quite low, especially in insect pollinated plants (1-5 grains per ovule, the upper limit being for anemophilous plants, Honig et al. 1992, Niesenbaum 1992, Herrera 2002 and 2004, Davis 2004).

The pollen to ovule ratio and the flowers to fruit ratio are two measures that quantify the pollination effort and the extent of fruit abortion (respectively), and are practical in quantifying a pollination system and give insights to the role of selfing versus outcrossing and to the pollination mode of the plants (Cruden 1977 and 2000, Stephenson 1981, Bawa and Webb 1984, Sutherland and Delph 1984, Sutherland 1986, Cohen and Dukas 1990, Ehrlén 1991, Spira et al. 1996, Burd 1998). The intensity of pollen tube competition, i.e. the numeral reduction from germinating pollen grains to pollen tubes at the bottom of the style, indicates the grade of sexual selection and to some extent the outcrossing level (Willson and Burley 1983, Schlichtling et al. 1990, Walsh and Chrlesworth 1992, Snow 1994, Erbar 2003, Németh 2005).

Deciduous forests and canopy research

Temperate deciduous forests in the northern hemisphere are the natural vegetation in most of Europe, eastern North America and eastern Asia (Röhrig 1991b). Due to tree habit, they contain a large biomass, many niches that allow animal diversity, influence the surrounding microclimate (and to some extent the global climate) and have a high recreational value (Röhrig 1991d, Schaefer 1991, Röhrig and Bartsch 1992, Stoutjesdijk and Barkman 1992).

Nowadays deciduous forests have been reduced to nature reserves in most of their distribution range (Röhrig 1991d, Peck 2001).

Temperate deciduous floodplain forests, i.e. humid forests along rivers going through lowland, have been especially decimated since early settlements were set on river banks and flooding has been regulated (Walter and Breckle 1986, Ellenberg 1996, Haase 2003). Today they exist in Europe only where intensively protected. This type of forest has an especially high biological and social value as they sustain a high diversity and are near to cities (Müller and Zäumer 1992, Röhrig and Bartsch 1992, Brown et al. 1997, Schmidt 2002).

A conservation of the complex forest ecosystem depends on the understanding of the natural processes governing it (Brown et al. 1997). An important process is the sexual reproduction of the trees, as it includes fruit production that is the basis for natural regeneration and sustains some of the fauna (Röhrig and Bartsch 1992, but see also Deiller et al. 2003). Details of the reproductive processes determine also such subtle characters as the genetic variability of the offspring, which may be crucial in enabling species to withstand natural pests (Richards 1997, Gehle and Krabel 2002, Küßner and Wagner 2002). In the last few years, the reproductive biology of the studied species has been intensively studied in the context of conservation biology with genetical tools (Bendixen 2001, Fromm 2001, Heuertz 2001, Morand et al. 2002, Höltken et al. 2003, Pandey 2005, Parolin et al. in press, see also www.ipgri.cgiar.org and www.fraxigen.net) but usually without a close look at the floral biology in the natural stands because of lacking accessibility.

Gender separation, especially monoecy and dioecy, are frequently found in temperate latitudes and especially in trees. These may be phylogenetically separated in three major groups:

1. Conifers – the phylogenetic oldest group (since carboniferous as a group, Magallon et al. 1999), either dioecious or monoecious (Givnish 1980), with specialized cone structure for wind pollination (Niklas and Paw U 1983, Niklas 1984 and 1992).
2. “Amentiferae” – e.g. Fagaceae, Betulaceae, a phylogenetic old group (since middle Cretaceous, Magallon et al. 1999), mostly including monoecious wind pollinated species with specialized catkins (aments, Faegri and van der Pijl 1966, Crepet 1981, Richards 1997).

3. "Newcomers" – genera of hermaphrodite, mostly tropically or subtropically distributed families, which present a range of sexual systems and pollination modes. Here belong the genera *Fraxinus*, *Acer* and *Tilia* (the families since uppermost Cretaceous or Tertiary, the genera since Palaeocene or Eocene, Manchester 1999)

Species of the genera *Fraxinus*, *Acer* and *Tilia* are typical trees of deciduous forests in the northern hemisphere (Röhrig 1991b, Lehrbuch der Botanik für Hochschulen 2002) that frequently grow together in natural forests in North America (Barnes 1991), Europe (Jahn 1991, Volk 2002) and East Asia (Ching 1991). In central Europe the species *F. excelsior*, *A. pseudoplatanus* (accompanied by *A. platanoides* and *A. campestre* in lower frequencies) and *T. cordata* have similar distribution ranges (Jahn 1991) and grow often together in natural forests, e.g. on slopes, on base-rich soils and in rich and wet habitats such as flood-plain forests (Jones 1945a and b, Wardle 1961, Jahn 1991, Pigott 1991, Ellenberg 1996). These species migrated back to northern Europe after the last ice age and present a high genetic variability, probably related to their migration from different refuges (Petit et al. 2003).

Canopy research concerns with the importance of the canopy as an ecosystem and its importance to global processes, that are evident on its size and structural complexity (Bassett et al. 2003). It is a young field, employing many different techniques to access tree crowns (Barker and Pinard 2001, Lowman 2001, Nadkarni 2001, Sutton 2001, Unterseher 2006). Construction cranes enable a constant and relative convenient access to large parts of the outer crown envelope. Canopy research has initially focused on silvicultural stands and on tropical rain forests (Ellenberg et al. 1986, Lowman and Wittman 1996, see review in Unterseher 2006), but lately turned to study temperate forests, especially in the context of their reaction to climate change (e.g. Körner et al. 2005). Canopy research in temperate forests concentrates on physiological processes, structural processes and biodiversity (Bredemeier et al. 2003, Häberle et al. 2003, Körner and Zotz 2003, Morawetz and Horchler 2003, Murakami and Hiura 2003, Shaw et al. 2003). Except for the study of the mating system of *Fraxinus lanuginosa* by Ishida and Hiura (1998 and 2002), reproductive biology of deciduous trees seems not to have been studied so far, and a comparative study aiming at the evolution of sexual systems and pollination modes has not yet been undertaken.

The studied species

The genera *Fraxinus*, *Acer* and *Tilia* are floral ecologically intriguing, as they originate from hermaphrodite, entomophilous ancestors and include species that span the range between entomophily and anemophily (Paw U and Hotton 1989, de Jong 1994, Wallander 2001) and species with much varying gender systems (hermaphroditism, monoecy, androdioecy, andromonoecy, polygamy and dioecy).

The genus *Fraxinus*, Oleaceae, includes 40-50 species in the northern hemisphere (temperate to subtropical, Lingelsheim 1920, Wallander and Albert 2000), many of which are important forest trees (Röhrig 1991b). Whereas the Oleaceae are mostly hermaphrodite insect pollinated species, *Fraxinus* includes anemophilous species that in fact comprise about two-thirds of the genus (Wallander 2001), and other breeding systems such as androdioecy, polygamy and dioecy, that were shown by Wallander (2001) to have developed independently in different species.

The genus *Acer* (Sapindaceae, APG II 1998, earlier regarded as Aceraceae in Sapindales, Pax 1902) comprises 111-156 species (range due to insufficiently known taxa, de Jong 1994), many of which are important forest trees in the northern hemisphere (Röhrig 1991b, mostly temperate and subtropical but reaching Java and Alaska, Oterdoom 1994a), and may have been such since the upper Cretaceous (Oterdoom 1994b) or at least since upper Eocene in Europe and in north America (Walther 1972, Wolfe and Tanai 1987). Sympatry and vicariance are typical to the genus (Wolfe and Tanai 1987, Oterdoom 1994a), hybridisation in natural stands is sometimes avoided by phenological differences (Oterdoom 1994a), but is in general possible and is achieved horticulturaliy in many garden variants (van Gelderen 1994a and b). The genus *Acer* includes mainly insect or wind pollinated monoecious species with different patterns of temporal separation of the genders, and some androdioecious and dioecious species (Ogata 1967, de Jong 1994, Verdú and Gleiser 2006).

The genus *Tilia* (Malvaceae, APG II 1998, earlier regarded as part of Tiliaceae in Malvales, Schumann 1890) comprises 10-50 species (range due to hybridisation, Fromm 2001) and is the only temperate genus, comprising important forest trees in the northern hemisphere (Röhrig 1991b), in its otherwise tropical to subtropical distributed family. *Tilia* species are regarded hermaphrodite and insect pollinated, however andromonoecy (Ito and Kikuzawa 1999) and wind pollination (Eisenhut 1957, Paw U and Hotton 1989) were also reported.

The studied species *F. excelsior*, *A. platanoides*, *A. pseudoplatanus* and *T. cordata*, can be placed along different ecological and morphological gradients in their common habitat, in addition to their places in the intragenric gradients. These gradients are the basis for their ecological comparison in the study, and are presented below.

Sexual system: *T. cordata* is hermaphrodite (Pigott 1991), *Acer* spp. are monoecious (de Jong 1994, males trees are also found, in a low frequency) and *F. excelsior* is polygamous and the closest to a full gender separation (Wallander 2001).

Pollination mode: *F. excelsior* is anemophilous (Wallander 2001), *Acer* spp. and *T. cordata* are entomophilous, considered to be pollinated by bees and flies (Müller 1873, Knuth 1898, Grube 1988, Binggeli 1992, Pigott 1991, Anderson 1976, Fromm 2001). However reports of wind pollination exist for *A. pseudoplatanus* (Pohl 1937, Binggeli 1992) and for *T. cordata* (Eisenhut 1957, Anderson 1976, indirectly in Hesse 1978 and 1979c, Paw U and Hotton 1989). Noticeably, the experimental evidence for wind pollination relies on exclusion experiments with a net of 1mm mesh size. Pollen in the air is reported for all three species (Rempe 1938, Hyde 1950, Anderson 1974).

Flowering phenology: *F. excelsior* flowers in early spring, before the leaves in the forest appear (March-April, Roloff and Pietzarka 1994), *A. platanoides* just before leaves in the forest appear (April, Lechowicz 1984 and 1995, Roloff and Pietzarka 1998), *A. pseudoplatanus* just after leaves in the forest appear (May, Jones 1945b), and *T. cordata* flowers at the beginning of the summer (June-July, Götz and Wolf 2004; see for all also Dierschke 1982 and Röhrig 1991c).

Dichogamy: *F: excelsior* is protogynous at flower level (Wallander 2001), individual trees of *Acer* spp. are either protandrous (or duodichogamous, i.e. flowering male-female-male) or protogynous (de Jong 1994), and sometimes display further variants (Haas 1933, de Jong 1976), and *T. cordata* is protandrous at flower level (Hildebrand 1869, Pigott 1991).

Flower morphology: *F. excelsior* has small flowers (2-4mm), male flowers consist of two stamens with large purple anthers and short filaments, female flowers consist of one pistil with a bilobed pink stigma, a style and an ovary with four ovules, of which only one usually develops to a seed, and hermaphrodite flowers are a combination of the two, with varying

organ sizes (Huldén 1941, Binggeli and Power 1991). Flowers of *A. platanoides* are medium (1cm) and of green-yellow color. Male flowers typically have eight stamens and no pistil, female flowers have short stamens with non-opening anthers and a pistil with a two-armed stigma, a style and an ovary with four ovules, of which usually two may become seeds (Buchenau 1861, Roloff and Pietzarka 1998). Flowers of *A. pseudoplatanus* are similar in structure but smaller, dully colored, with larger stamens and stigma (Semm 1966, de Jong 1976, Grube 1988). *T. cordata* has medium flowers (1-1½ cm, Eisenhut 1957, Götz and Wolf 2004) that are white to yellow with 15-30 stamens with bithecate anthers and a pistil with a five lobed stigma (Götz and Wolf 2004), a style and an ovary with ca. ten ovules, of which usually one turns into a seed (Eisenhut 1957).

Inflorescence morphology: *F. excelsior* inflorescences are sitting upright panicles of 80-300 flowers, whereas male inflorescences include more flowers than hermaphrodite and female inflorescence (Rohmeder 1952, Bredehöft 1985, Wallander 2001, Tal 2003 up to 700 flowers in male inflorescences). Male inflorescences are often turned into spangle galls by an eriophyoid mite (Buhr 1964, Castagnoli 1996, Westphal and Manson 1996). *A. platanoides* inflorescences are more or less upright umbel-like compound inflorescences (termed corymbose by Oterdoom and de Jong 1994, a loose broad panicle by Ogata 1967), with ca. 40 flowers (Semm 1966). The unfolding of the inflorescences goes hand in hand with the anthesis of consequent gender phases (Haas 1933). Inflorescences of *A. pseudoplatanus* are hanging (pendulous) and elongated (termed racemose-paniculate in Oterdoom and de Jong 1994, elongated compound inflorescence with reduced cincinni in de Jong 1994, or an elongated panicle in Ogata 1967). They include ca. 70 flowers (Semm 1966, Binggeli 1992). *T. cordata* inflorescence is a corymb-like botryoid dichasium (Eichler 1878) or a pleiochasium with 3-11 (-16) flowers (Götz and Wolf 2004).

Insertion of the inflorescences on the twig. *F. excelsior* inflorescences are inserted laterally on the twig, a state typical to anemophilous *Fraxinus* species in contrast to entomophilous ones which have terminal inflorescences (Wallander 2001). Inflorescences of both *Acer* spp. unfold from terminal buds on the twigs, from which also leaves unfold. Ogata (1967) argues that in the genus *Acer*, terminal inflorescence are usually compound and accompanied with one to three pairs of leaves, whereas lateral inflorescences are usually simpler, have no accompanying leaves and characterise species that tend to wind pollination and gender separation (along the gradient andromonoecy – androdioecy – dioecy). *T. cordata*

inflorescences are accompanied by a bract and unfold from lateral buds on new twigs (Schumann 1890).

Nectar production: *F. excelsior* produces no nectar (Wallander 2001), *Acer* spp. have a nectar producing disc (Sprengel 1793) and secret between 0.5 mg per day (*A. platanoides*) and 1 mg/day (*A. pseudolatanus*, both in Haragsim 1977). *T. cordata* flowers have nectar glands on the sepal basis that are covered with hairs (Fromm 2001) and secret 0.5-5mg/day (Kleber 1935, Beutler and Wahl 1936, Eisenhut 1957, Anderson 1976, Pigott 1991, details in Corbet et al. 1979).

Pollen morphology: Hydrated pollen size of *F. excelsior* is 22-27.5µ in diameter, of *A. platanoides* 25-30µ, of *A. pseudoplatanus* 30-35µ and of *T. cordata* 25-36µ (the range represents different authors - Lingelsheim 1920, Erdtman 1952, Eisenhut 1957 and 1961, de Jong 1976, Grube 1988, Binggeli 1992, Wallander 2001, the data of different sources diverge considerably, although the individual authors mostly state a much smaller standard deviation of their measurements, probably after different preparation methods). Dehydrated pollen grains are in form of a barrel in *F. excelsior*, of a wheat grain in *Acer* spp. and disc to dome shaped in *T. cordata* (http://paldat.botanik.univie.ac.at). The fall speed of the pollen is 2-4cm/sec for all species (Eisenhut 1961).

Pollen of *F. excelsior* is powdery, pollen of *A. pseudoplatanus* and *T. cordata* is sticky when very fresh and becomes powdery after a few hours, and pollen of *A. platanoides* is sticky (Hesse 1978, 1979a-c). Hesse found that the difference in the stickiness of the pollen grains does not result from the existence or absence of pollenkitt *per se* as it is produce in large amounts in all species, but from the fate of the pollenkitt in the loculus and on the pollen grains (Hesse 1981 as a general rule for the change to anemophily). In *F. excelsior* the pollenkitt is filtered within the loculus by the peripheral grains (Hesse 1979a) and in *A. pseudoplatanus* and *T. cordata* it is mostly caught underneath the pollen upper surface (tectum) or between the baculae, respectively, and thus does not cause stickiness. In *A. platanoides* the pollenkitt is smeared on the surface of the pollen grain in a thick and uniform layer (Hesse 1979b). He interprets the powderiness of pollen of *A. pseudoplatanus* in combination with the hanging position of the inflorescence both as promoting some wind dispersal of pollen and as enabling the sprinkling of a visiting insect with pollen (Hesse 1979b).

Pollen number and P/O (pollen to ovule) ratio: Pollen numbers per flower are in *F. excelsior* 20,000-60,000 for male flowers, 6,000-30,000 for hermaphrodite flowers (Bredehöft 1985, Molina et al. 1996, Wallander 2001), in *A. platanoides* 15,000 (Grube 1988), in *A. pseudoplatanus* 35,000 (Grube 1988) and in *T. cordata* 43,500 (Hyde and Williams 1945, Pigott 1991, probably both cite Pohl 1937). *F. excelsior* and *T. cordata* usually have one seed per flower, so that their P/O ratios per hermaphrodite flowers are the same as the pollen number per flower (Fromm 2001). The *Acer* spp. usually have two seeds per flowers, thus P/O ratios for a male versus a female flower are the half of the pollen number per flower. P/O ratios at inflorescence level (Harder et al. 2004), taking into account the numeral relation of male and female flowers are presented in the results. The frequently cited Pohl 1937 presents pollen per anther values for *F. excelsior* and *Acer* spp. that are clearly underestimated (Bredhöft 1985, Grube 1988, Wallander 2001) and are thus ignored. For *T. cordata* these are the only values I found. Also his assumed flower number per inflorescence for *A. pseudoplatanus*, ca. 1000, is clearly exaggerated.

Stigma morphology: Stigmas of all the species are of the dry type (Heslop-Harrison and Shivanna 1977). They have two short lobes in *F. excelsior*, two long lobes in *Acer* spp. (surfaces in both genera are with unicellular papilla, very short in *F. excelsior*, long in *Acer* spp., Schill et al. 1985, Grube 1988, Peck and Lersten 1991) and five short lobes in *T. cordata* (surface described as multicellular, multiseriate papillate by Heslop-Harrison and Shivanna 1977 but as non-papillate by Schill et al. 1985). Stigma area in *F. excelsior* is ½-1mm^2 (Tal 2003), in *Acer* spp. stigmatic area is larger in *A. pseudoplatanus* than in *A. platanoides* as are also the size and density of the papillae (2.2mm^2 with 25, 97µ long papillae per 10µ^3 versus 1mm^2 with 16, 56µ long papillae per 10µ^3, respectively, Grube 1988). Stigma area in *T. cordata* is 1.9mm^2 (Eisenhut 1957). The pollen to stigma surface ratios (Eisenhut 1957, Cruden 2000) per flower are thus ca. 50,000, 15,000, 16,000 and 23,000 for *F. excelsior*, *A. platanoides*, *A. pseudoplatanus* and *T. cordata*, respectively.

Fruit and seed: All species are anemochorous (wind dispersed), with a flight accessory (fruit wings in *F. excelsior* and *Acer* spp., an infructescence bract in *T. cordata*, Leins 2000). These accessories are green during fruit development and probably contribute assimilates to the developing fruit (Eisenhut 1957, Bazzaz et al. 1979). *F. excelsior* and *T. cordata* usually have one seed per fruit, rarely two or three (Huldén 1941, Eisenhut 1957) in *Acer* spp. one fruit parts to two mericarps which are the diaspores, each with one seed. Fruit of *Acer* spp. and *T.*

cordata were found to be up to 50% and 100% empty (respectively) in different studies (e.g. Jones 1945b, Eisenhut 1957, Pigott and Huntly 1981, Binggeli 1992, de Jong 1994). Fruit and seed weights are around 150µg and 100µg in the *Acer* spp. and around 50µ and 30µg in both *F. excelsior* and *T. cordata* (ranges after different authors: *A. platanoides* dry fruit weights 80-290µg, fresh up to 360µg, seeds dry weight 30-150µg, *A. pseudoplatanus* dry fruit weights 90-220µg, fresh up to 350µg, seeds dry weight 45-135µg, Acatay 1928, Jones 1945b, Semm 1966, Hong and Ellis 1990, fruit and seeds of protogynous trees are heavier than of protandrous trees in both species after Semm 1966; *F. excelsior* dry fruit weights 45-80µg, fresh up to 102µg, seeds dry weight 12-63µg, Acatay 1928, Binggeli and Power 1991; *T. cordata* dry fruit weights 35-40µg, fresh up to 70µg, seeds dry weight 10-65µg, Acatay 1928, Pigott 1991, Fromm 2001). *F. excelsior* may produce up to 1-1,5 million fruit per year per hectare (in masting years, Gardner 1977, Tapper 1996), *T. cordata* up to 100-150,000 per year per hectare (Pigott 1991). Reported fruit to flower ratios are between 1:2 for *F. excelsior* and 1:6 for *T. cordata* (cited in Sutherland and Delph 1984).

To summarise, the studied species present a gradient in the general characteristics of their sexual systems (gender separation, pollination mode) as well as in their phenology and morphology of flowers and inflorescences. These characters have long been discussed in terms of a change from insect to wind pollination, but usually in a taxonomical context (Hall 1951, Semm 1966, Ogata 1967, de Jong 1976 and 1994, Grube 1988, Paw U and Hotton 1989, Wallander 2001) and not by comparing the detailed reproductive biology of the species in one habitat. This is understandable, as inflorescences of these trees in their natural habitats are located on thin twigs at 30m height (Lowman and Wittman 1996).

Aims of the study

The study was planned to compare the reproductive biology of the species from an ecological perspective, in order to gain a new look at the evolution of their sexual systems and pollination modes. It thus aimed at gaining detailed information about the reproductive biology of the species, including their gender separation, flowering phenology, pollination and fruit production. Emphasis was put on using crown accessibility to study differences within the crowns and the study of all canopy trees was aspired to in order to encompass as much variability as possible. Further, the effects of microclimate and the role of small arthropods in the reproductive biology were study aims.

Methods

The study site, the crane

The study took place in Leipzig's floodplain forest (Germany), a semi-natural deciduous forest. The forest has been used by man since 650 years at least (Lange 1959) using different forestry practices. The major changes it underwent in the last 150 years are:

1. Being left to grow higher by abandoning the practice of cutting down all trees but oaks every 10-15 years (Lange 1959, Sickert 2003b, this last form of silviculture is termed "coppice with standards" Röhrig 1991d, or "Mittelwaldwirtschaft", Ellenberg 1996).
2. River regulation reduced and later prohibited regular flooding of the forest, thus drying it gradually (Brown et al. 1997, Sickert 2003b).

These influences resulted in a higher forest with a full canopy closure, and an upcoming of the tree species *Fraxinus excelsior* and *Acer* spp., mainly *A. pseudoplatanus*, which are, together with *Tilia cordata* the dominating crown species of the study site (Seele 2004).

The study site is the plot of Leipzig's floodplain forest crane (Leipziger Auwaldkran, LAK), at the northern edge of the "Burgaue" (51°20'16''N, 12°22'26''E), 102m above sea level, mean annual temperature 8.8°C (mean for the coldest month January is 0.2°C, for the warmest month July 18.7°C, Sickert 2003a), mean annual rainfall 512mm, soil is nutrient-rich loamy alluvial, the vegetation is classified as Querco-Ulmetum (Müller and Zäumer 1992, Morawetz and Horchler 2003).

The plot is 1.6 hectare large, its canopy is reachable up to 32m height using a crane (Liebherr 71EC) with a 45m long jib that can move on a 120m long rail. The research was done from a gondola from which the movements of the crane were remote-controlled. The gondola is about 1m in diameter and can be quite exactly manoeuvred so that the most of the crown surface could be reached and delicate actions could be taken.

The study years were 2003-2005, the duration and frequency of observations were every 1-4 days, 5-6 hours at a time, during flowering period (March to July). Additional crane time was used for structural studies in August-September and for fruit collection in late September. Results from 2002 that are presented are a further analysis of the data of my diploma (Tal

2003). Methods, data and discussion to the studies of structure and climate are presented in the appendix.

The studied trees

The studied trees, *Fraxinus excelsior*, *Acer platanoides*, *Acer pseudoplatanus* and *Tilia cordata* are the dominating species in the plot (Seele 2004). Practically all canopy trees of these species were studied (table 1, see also figure 42 in the appendix and plate 1). Each tree was referred to by a unique shorthand and the data for individual trees may be obtained from the author. In the results the notation of these shorthands was left out.

Table 1: Number of studied trees after species, year of study and theme. Intensity of flowering and number of fruit include non-flowering and non-fruiting trees (respectively).

Species and year / theme of study	tree gender	intensity of flowering	flowering time	number of fruit
F. excelsior 2002	68	69	38	21
F. excelsior 2003	64	64	48	21
F. excelsior 2004	66	71	63	21
F. excelsior 2005	91	97	90	27
A. platanoides 2004	8	8	8	8
A. platanoides 2005	6	10	1	10
A. pseudoplatanus 2004	53	50	53	47
A. pseudoplatanus 2005	60	83	65	74
T. cordata 2004	9	30	9	30
T. cordata 2005	9	30	9	30

Detailed investigation was limited to the largest trees of each species. Tree sizes are analysed in the appendix, here the median and maximal size parameters (stem diameter, height and crown area) for the trees of the studied species are presented (table 2).

Table 2: Sizes of the trees of the studied species (all trees are canopy trees). Data for tree height and stem diameter were taken from Seele (2004), for data for crown area see appendix.

	canopy trees: median (maximum) of		
	stem diameter (dbh, cm)	tree height (m)	crown area (m^2)
F. excelsior	59 (93)	30.4 (34)	50 (230)
A. platanoides	55 (91)	24.6 (32)	80 (165)
A. pseudoplatanus	41 (78)	26.5 (31.5)	20 (90)
T. cordata	36 (93)	26.7 (31.4)	25 (120)

The range of the ages of the trees is coarsely estimated to be between 50 and 200 years (Lange 1959, see figure 41 in the appendix).

Gender and phenology

Fraxinus excelsior

Gender

The following definitions were used to determine flower, inflorescence and tree gender type (after Wallander 2001 and Tal 2003, somewhat modified).

Categories for flower gender (plate 2) were:

1. Male – large stamens (anthers ca. 2mm long, rarely with a rudimentary sterile pistil).
2. Male-biased hermaphrodite – large stamens, a small pistil with thin stigma lobes (spread in anthesis).
3. Balanced hermaphrodite – a large pistil (thick stigma lobes, stigma swollen in anthesis), medium size stamens (anthers ca. 1mm long).
4. Female-biased hermaphrodite – a large pistil, small (fertile) stamens.
5. Female – a large pistil, no or rudimentary (sterile) stamens.

The inflorescence gender types (plate 3) were:

1. Male – only male flowers

2. Mainly male – most flowers male, some male-biased hermaphrodite flowers (ranging 1-50 in number, usually around 10).
3. Male-biased hermaphrodite – male-biased hermaphrodite flowers as a large minority or a small majority in the inflorescence, the rest of the flowers are male.
4. Balanced hermaphrodite – balanced hermaphrodite flowers, possibly with some female flowers at a basal position in the inflorescence.
5. Female-biased hermaphrodite – mainly female-biased hermaphrodite flowers with some female flowers, usually with rudimentary stamens.
6. Female – female flowers (mostly without rudimentary stamens).

Tree gender types were determined after the combination of inflorescence gender types as one of the categories:

1. Male – with only male inflorescences
2. Male with few hermaphrodite flowers - with male and mainly male inflorescences, less than 1% hermaphrodite flowers from total flowers on tree (in the overview, this category includes trees that were categorised as either male with few hermaphrodite flowers or as male in different years).
3. Male-biased hermaphrodites – with male, mainly male and male-biased hermaphrodite inflorescences, between 10% and 50% hermaphrodite flowers from total flowers on the tree (in the overview, this category includes trees that were categorised as either male-biased hermaphrodites or male in different years).
4. Balanced hermaphrodites – mostly balanced hermaphrodite inflorescences. May include some male-biased hermaphrodite or female-biased hermaphrodite inflorescences.
5. Female-biased hermaphrodites – mainly female-biased hermaphrodite inflorescences (in the overview this category includes trees that were categorised as either female-biased hermaphrodites or as balanced hermaphrodites in different years).
6. Females – mostly female inflorescences. May have some female-biased hermaphrodite inflorescences.

Embryonic flowers were studied by collecting twigs before and at beginning of flowering and dissecting their buds. About 20 twigs were collected of trees of different genders in 2005.

Phenology

The flowering intensity per tree was defined as full, partial (about a half of the twigs with inflorescences), scant (less than 10% of the twigs with inflorescences, usually one or two branches) or not flowering.

The categories for the phenological stages of flowers were the following:

1. Male flowers.
    a. Anthers closed.
    b. Anthers open (dehiscent), with pollen.
    c. Wilt, anthers open without pollen, brown.
    d. Frost damage – anthers brown, not dehiscent.
2. Hermaphrodite flowers (all types).
    a. Stigma small and dark.
    b. Stigma exposed, purple (in male-biased hermaphrodites lobes spread).
    c. Stigma exposed, pink (in hermaphrodites and female-biased hermaphrodites swollen to different grades), anthers closed.
    d. Stigma exposed, pink, anthers dehiscent.
    e. Anthers dehiscent, stigma wilt (shrivelled, dark).
    f. Wilt, anthers empty.
3. Female flowers – like stages **a** to **c** in hermaphrodite flowers, finally wilt.

Stigmas were receptive in stages **b**, **c** and probably **d**. The peroxidase test (using Peroxtesmo KO peroxidase test paper after Dafni 1992) showed false positives and had to be considered unreliable in this case. Stigmas in stage **b** were found to support germinating pollen in probes that were fixated in the field. It is conceivable that pollen landing on stigmas in stage **a** stayed there till the stigma was receptive, and then germinated, so that stage **a** already functions as pollen capturing.

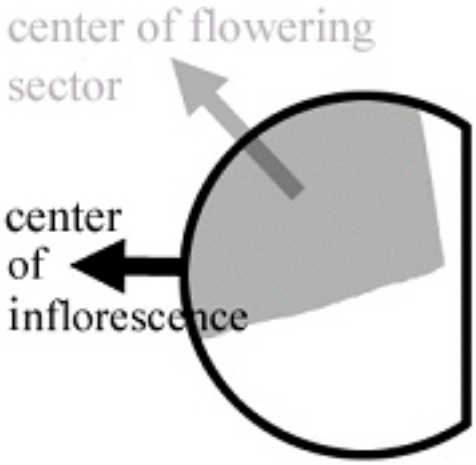
Inflorescence phenology was categorised to the following stages (plate 3):

1. Male inflorescences:
    a. Bud opening:
        i. Initial opening - anthers partly visible.

   ii. Complete opening – inflorescences looks like a purple knob of ca. 2 cm in diameter

b. Anthesis:
   i. Initial – opening of anthers, expressed as a percent of the inflorescence, optically assessed. Lengthening of the inflorescence facultative. Color of dehiscent part bright yellow (pollen).
   ii. Advanced – a mix of closed, dehiscent and wilt anthers. In detailed investigation expressed as percent of the inflorescence after the color of these parts (purple, bright yellow and greenish-yellowish brown respectively).
c. Wilt: All anthers open and empty, only traces of pollen, color greenish to matt brown.
d. Frost damage: Inflorescence or inflorescence parts bright brown, anthers keep their form.

To study the aspect of anthesis, the azimuth of the center of the flowering sector and of the middle axis of the inflorescence were measured (after one of 16 wind directions) according to the figure to the right. This was done on four male trees at different stages of overall anthesis in 5-10.4.2004, and included 256 inflorescences on 31 twigs (twigs were selected randomly, all inflorescences on each twig were checked).



2. Mainly male, and male-biased hermaphrodite inflorescences:
   a. Bud opening: Initial opening – anthers partly visible, stigmas with closed lobes, dark.
   b. Female anthesis: Complete opening of the bud - the inflorescence looks like a purple knob of ca. 2 cm in diameter, with stigmas projecting with spread lobes. Duration and persistence of the stigmas depending on inflorescence type (stigma stature and number of hermaphrodite flowers).
   c. Male anthesis as in male inflorescences, stigmas still seem receptive at the beginning of male anthesis, then wilt.
   d. Wilt and frost damage the same as male inflorescences. Frost damage to stigmas was seen by their early disappearance.

3. Hermaphrodite inflorescences:
    a. Bud opening, exposition of dark stigmas, not receptive.
    b. Female anthesis: Exposition of ever more stigmas of the lengthening inflorescence, the stigmas become purple and then pink, and swell. In detailed investigations quantified by the length of inflorescence and approximate number of exposed stigmas. An inflorescence at an initial flowering stage was ca. 1-1.5cm long, and most stigmas were exposed at inflorescence lengths of 2-4cm. Beginning with 4cm most stigmas were wilt (exact lengths depended on inflorescence gender, see Tal 2003).
    c. Male anthesis: Opening of stamens, quantified as percent from the inflorescence. Stigmas become wilt (also quantified as approximate proportion), before the end of male anthesis.
    d. Wilt: Anthers empty, stigmas wilt.
    e. Frost damage – stigmas become black, shrivelled and hard. Quantification of the proportion from exposed stigmas (i.e. basal flowers that are not directly seen were not including in total). Frost damage to male flowers as above.
4. Female-biased hermaphrodite and female inflorescences:
    a. Female anthesis as in hermaphrodite inflorescences, usually female anthesis starts already at bud opening stage, in which stigmas are already pink and somewhat swollen.
    b. Male anthesis is just recorded as occurring or not due to its limited scope.
    c. Frost damage as in hermaphrodite inflorescences.

Acceleration of phenology of inflorescences on a twig was achieved by covering it with a paper bag tightened to the twig with a cable tie. This also enabled a comparison in vivo of frost damage to inflorescences of different lengths on one hermaphrodite tree. Frost damage was assessed as the proportion of damaged stigmas from all stigmas in the inflorescence and compared with exposed inflorescences on the same branch that were in the same flowering stage prior to covering.

The following stages of tree phenology were defined. Anthesis in the tree was quantified in different accuracy grades, depending upon field-time limitations. As a rule, the bigger trees

received more attention than the smaller trees. The frequency of checks was taken to complete a survey of the stand (taking 1-2 field days) two to three times a week.

1. Male trees:
    a. Before anthesis - Bud stage, initial and complete opening of buds, judged after the majority of inflorescences (opening one and two of Tal 2003, detailed results left out here).
    b. Anthesis assessed as percent of total flowers on the tree in two accuracy levels:
        i. Tree based (coarse) – a visual assessment, assisted by the conspicuous coloration of inflorescence portions and by the commonly uniform anthesis from southern to northern aspect. The assessment was done after inspecting the tree crown from different aspects and different heights and was occasionally controlled by a more accurate assessment. The estimated error is ±20% of flowering.
        ii. Twig based (fine) – 3-4 height layers of the crown were represented by sampling 20-40 twig from each, then averaging anthesis for the twigs and averaging crown parts with appropriate weights for the whole tree (further details on quantitative assessment of the number of twig in Tal 2003). The estimated error is ±10% of flowering.
    c. For the phenology diagrams of the stand, these percent-based assessments were reduced to the categories main flowering (10%-90%) and residual flowering (<10% or >90%) for each tree.
2. Male-biased hermaphrodite:
    a. Female anthesis was noted for the stage corresponding to complete opening of buds in male trees. Its intensity was classified as low (up to 10 stigmas per inflorescence, not on all inflorescences) or high (10-50 stigmas, on most inflorescences).
    b. Male anthesis as in male trees.
3. Balanced hermaphrodite, female-biased hermaphrodite and female:
    a. The female anthesis was judges after the commonest inflorescence stage (relying on their length and color). The tree was defined to be in an initial stage when most exposed inflorescences were in an initial stage, and to be in a final stage when most stigmas were wilt. Between these stages the tree was regarded to be in its main flowering stage.

b. Male anthesis was noted as occurring or not. The overlap of female and male flowering is not represented in the phenology diagrams.

The trees were ranked each year after the starting date of the main flowering (reaching 10% of total in males and being after the initial phase in hermaphrodites). Trees with equal dates were ranked after the date of starting of overall flowering and if this was also equal, after the percent of anthesis in later checks. A normalized rank in each year was calculated by dividing the rank by the number of ranked trees.
The start and end dates as well as flowering durations were taken for the overall flowering and for the main flowering separately, and the correlations and regressions among them, for all trees and in respect to tree gender, were calculated using common statistical tests (SigmaStat 3.0® was used for all statistical tests). The number of trees in anthesis at each check and the accumulating number of flowered trees were summed after the period of overall flowering. The measures for the synchrony of flowering among the trees are presented below, in the synchrony section.

Covering twigs with paper bags (tightened to the twig with cable ties) was applied to twigs in 2004 and 2005 as an attempt to accelerate their flowering phenology. The microclimate of such bags was studied simoultaniously and the effect achieved in *F. excelsior* was used to assess the sensitivity of flowering phenology to microclimate and to compare frost susceptability after inflorescence, as well as enable controled exposure of virgin stigmas and pollinator exclusion. Similar covers were applied for the other species.

Vertical patterns in the initial phases of leaf unfolding (bud to fully spread leaves) were recorded on the studied *F. excelsior* and *A. pseudoplatanus* in 2005. The stages leaf buds closed, buds opening, leaves begin to unfold, advanced unfolding and spread leaves were distinguished. Trees with a clear vertical gradient in the unfolding of the leaves were considered those that had a difference of at least two stages between crown bottom and crown top during the unfolding process.

Acer platanoides

Tree gender sequences of *A. platanoides* were determined by following the gender of flowers in anthesis every one to four days.

Flowering phenology within the crown was studied by marking branches at three heights before flowering and checking the number of open flowers per inflorescence, their gender and the length of the inflorescence every several days. The branches were also marked radially from the stem outwards every 20 cm, so that the inflorescences of each branch were classified after their horizontal location in the crown's envelope. The inflorescence length was measured from bud base to most distant flower at accuracy of 0.5 cm (plate 6). The surroundings of the branches were inspected for branches presenting a different gender. The results are presented for one big tree, the branches were at heights 30m (a shoot at the upper boundary of crown), 24m (middle of crown) and 16m (lower boundary of the crown, near a large gap in the stand).

Acer pseudoplatanus

Tree gender sequences were determined by following the phenology of the trees as described below, and classifying them as protandrous or protogynous (figure 1, to the left and to the right respectively). The area studied in 2004 was 1.3ha (the southernmost part of the plot was not studied), in 2005 the whole plot was studied. The data from 2003 is fragmentary and was left out.

The number of flowers in each phase was assessed in 13 protogynous trees and 37 protandrous trees in 2005, by counting them on a few large inflorescences. After this crude estimation flower number was categorised at each stage in one of the categories: 1-5, 6-10, 11-20, 21-30, 31-40, 41-60, 61-80, 81-100, 101-120, and these were compared for protogynous vs. protandrous trees at their female, first male and second male phases.

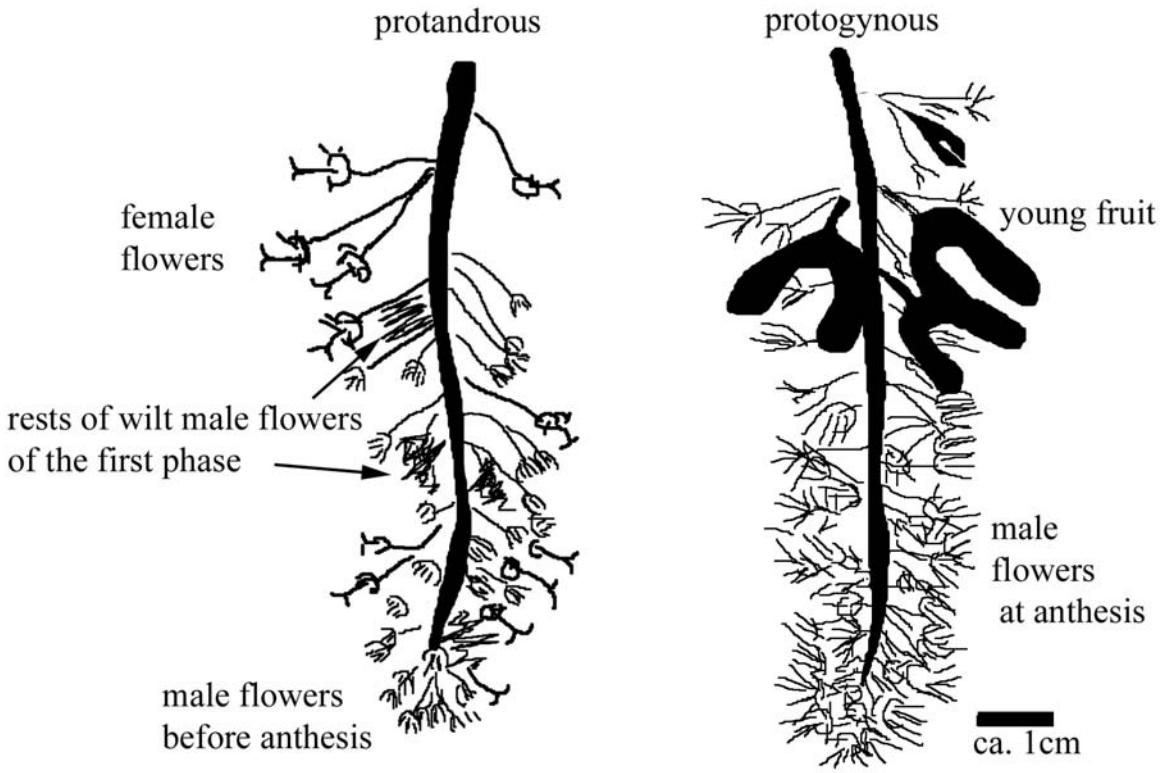
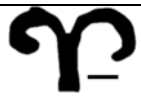
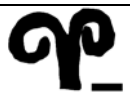


Figure 1: The two common types of inflorescences in *Acer pseudoplatanus* drawn schematically after photos (see plate 5). To the left a protandrous (duodichogamous) inflorescence, in which the first male stage is already wilt and mostly fallen (rests are marked by arrows), flowers of the female phase at anthesis and flowers of the second male phase still develop (stamens short). To the right a protogynous inflorescence, in which flowers of the female phase already develop to fruit and flowers of the male phase are in anthesis. Stamens are represented as strokes (long strokes for male anthesis), the number of flowers is somewhat reduced. The bar represents ca. 1 cm.

The gender and the stage of flowering were checked in 2-3 branches (20-30 inflorescences) in the upper canopy every few days. The stages of flowering in a single flower were determined after the state of stamens in male flowers (filament length, anther opening and presence of pollen) and after the stigma form in female flowers (the grade to which its lobes were spread). The stage of flowering in an inflorescence was determined after the proportion of male flowers in anthesis (male phase) and after the state of most female flowers (female phase), as summarised in table 3.

Table 3: Phenological stages for flowers and inflorescences in the male and in the female phases. Illustrations of style and stigma as sillouhettes after fotos (plate 5). Bars approximately 1mm.

flowering phase	male anthesis		female anthesis	
	flower	inflorescence	flower	inflorescence
		percent of open flowers		form in the majority of flowers
pause	young – filaments short	0	young – style short	
	before anthesis – filaments long, anthers closed	0	before anthesis – style long, lobes unspread	
marginal	anthesis – open anthers with pollen	10%	anthesis start – lobess start spreading (<1mm)	
main flowering phase		1/3	anthesis – stigma lobes clearly detached	
		1/2	anthesis – stigma lobes clearly detached, longer (about 3 mm)	
		2/3	anthesis end – lobes start to role backwards, older	
marginal		90%	anthesis end – lobes curled (in some trees)	
pause	wilt – anthers brown and empty	100%, wilt	wilt – stigmas darken	
	stamens fallen		stigma fallen, young fruit	

The flowering stage of the tree was taken to be that of most large inflorescences. The phenology diagrams present the gender phases at main and overall duration (i.e. without and with the marginal stages, respectively). Analysis of flowering dates, duration and synchronisation are based on these two periods.

Comparisons of anthesis at different heights in the tree were done by repeating the check at lower crown. A difference was concluded if the results differed in two stages of table 3 at least. The data are presented as the number of comparisons affirming the hypothesis that lower crown flowered ahead of upper crown, from a total of 64 comparisons on 24 trees in 2004 and 47 comparisons in 2005.

The flowering intensity per tree was defined as full, partial (about a half of the twigs with inflorescences), scant (less than 10% of the twigs with inflorescences, usually one or two branches) or not flowering. Herbivore damage were categorised per gender phase as light (damage of up to ca. 30% of the flowers) or heavy (50-100% of the flowers damaged). Different types of damage were not distinguished.

Synchrony measures

The main measure for the synchrony among the trees was Primack's (1980) synchronicity index that is the sum of the percent of overlap in flowering phenology over all pairs of trees in the population, divided by the number of pairs – $(\Sigma_{pairs} a/b) / (n \cdot (n-1)/2)$, in which the percent of overlap for each pair is taken as the ratio between the duration of their common flowering – **a**, and the shorter flowering duration of the two – **b**, and **n** is the number of trees. This index is one for an overlap of all trees and zero when none of the flowering periods overlap. It was calculated in *F. excelsior* for the overall flowering periods, for the main flowering periods, for all trees and for trees of reciprocal gender only. The synchronicity index was calculated in *A. pseudoplatanus* for the overall flowering duration in each gender phase of protandrous and protogynous trees separately and also of pairs of these gender phases.

The synchronicity index is a decreasing function of the number of trees (**n**) for a constant degree of overlap (figure 2), because the number of overlapping pairs increases linearly with **n** and the number of pairs in the denominator increases as $\mathbf{n^2}$. To avoid this dependancy, a second index, the step, was calculated assuming a sequence of periods of a constant duration, each beginning (and ending) a constant interval of time after its predecessor. The ratio of this interval to the total duration (termed the step, **s** in %) is independent of the number of trees and is an intuitive characteristic of the phenological pattern.

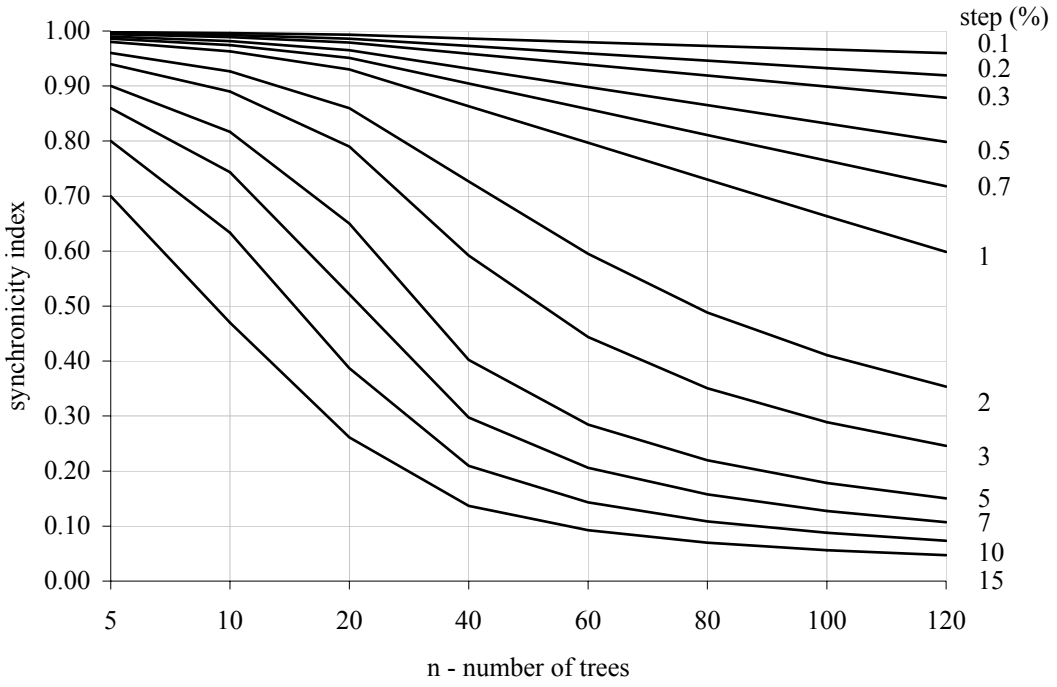


Figure 2: The synchronicity index's dependency on tree number for different steps in abstract phenology diagrams.

The step was calculated from the synchronicity index and the number of trees backwards in the following way. The synchronicity index was calculated for abstract phenological diagrams of equal flowering durations and a constant interval, or step, from each flowering period to the next. The diagrams contained between 5 and 120 trees (overall 20 values) and had a step from 0.1% to 30% (overall 60 values). They were used to create a relationship among tree number, synchronicity index and step similar to figure 2, but with a higher density of curves. The step was taken for the real phenologies as the closest one for the corresponding tree number and synchronicity index. The step was calculated for the same combinations of flowering period as for the synchronicity index, except for *F. excelsior* of reciprocal gender (as the number of trees is not definable) and for *A. pseudoplatanus* between gender phases of the same tree group (as the distribution of flowering periods is bimodal – either much overlap or no overlap, thus strongly violating the uniformity assumption in the abstract phenology diagrams).

Three additional measures for synchrony were compared to the former: (1) The ratio of average duration to the standard deviation of starting times (see Bolmgren 1998). Two modifications of Primack's synchronicity index: (2) The commonly used measure (Σ_i ($\Sigma_j e_{j\neq i}$) / f_i) / (n·(n-1)), in which $\mathbf{e_{j\neq i}}$ denotes the overlap of the i^{th} and j^{th} trees, $\mathbf{f_i}$ the duration of flowering of the i^{th} tree and **n** the number of trees (Augspurger 1983, Gómez 1993, Bolmgren

1998, tree pairs are counted twice and are divided first by the duration of the one, then by the duration of the other instead of counting each pair once and dividing by the shorter duration of the two as in Primack 1980). (3) Albert et al.'s (2001) modification – $(\Sigma_i \ (\Sigma_j a_{ij} / b_{ij})) / (n \cdot (n-1))$, in which $\mathbf{a_{ij}}$ denotes the overlap of the i^{th} and j^{th} trees and $\mathbf{b_{ij}}$ denotes the time in which one of them at least flowered (counted only for $i \neq j$) and **n** denotes the number of trees. This index is in general smaller than the synchronicity index as its denominators (the b_{ij}'s) are larger. These measures were calculated for the same cases as the synchronicity index.

Tilia cordata

The different flower forms that were found are described in the results section as *T. cordata* is considered hermaphrodite by all authors studying it (Eisenhut 1957, Pigott 1991, Fromm 2001). Gender of flowers was recorded in six trees in 2003 and nine trees in 2004 and 2005 (some of the trees recurring). Flower gender was determined on marked branches (with 20-30 inflorescence each) over the flowering period and in alcohol probes in 2003, by occasional observation in 2004 and quantitatively in checks in 2005 (see below). The number of buds per inflorescence was recorded in a branch system including in median 47 inflorescences (total 1673 inflorescences) in 2004, and median 60 inflorescences (total 752 inflorescences) in 2005.

Flowering intensity in 2005 was categorised as full, partial (less than a half of the crown) or no flowering. Flowering phenology was followed in checks of twig systems in crown top during the flowering. In each check flowers were categories after their flower form (see results, figure 28, plate 7) and flowering stage: Before during or after male anthesis according to the state of most anthers (closed, open with pollen or open and empty, respectively) and before during or after female anthesis according to the state of the stigma (lobes closed, lobes spread and wilt respectively). Overall 45 checks with median 33 inflorescence (137 flowers) per check were done (total 1610 inflorescences, including some comparisons with lower crown). To express the extent of gender overlap in a check, the percent of flowers in male anthesis was compared to the percent of flowers in female anthesis, and the smaller of the two was divided by the larger of the two. This ratio is one when the same proportions of flowers are male and female, and is zero when all flowers flower with the same gender.

The dependence of the beginning of flowering on the aspect and height in the crown was studied in 2004. In each of eight compass points and three heights three small branches were chosen to represent the common, minimal and maximal flowering stage. The beginning of flowering is presented, in which the flowering stages were swollen buds (markedly larger than others, but petals not visible), opening buds (petals visible but not fully spread) and open flowers (petal fully spread, plate 7). In 2003 the flowering phenology was followed in marked branches on two trees by counting the flowers in from each type and in each step (ca. 700 flowers per tree).

Pollen, visitors, pollination and fruit

Pollen size

Flowers were collected in 2005 at treetop and within a few hours pollen was taken from freshly opened anthers (2-3 anthers of 2-3 flowers), put on a slide, and observed in dry state. Then a drop of water was added, a rush hydration occurred, after which arbitrary sections of the probes were photographed with the focus on the outer circumference of the grains at a x400 magnification. Later the diameters of the grains (in *T. cordata* the longer axis, only for pollen in equatorial view, Erdtman 1952) were measured using Photoshop® - a scanned ruler was calibrated with its image that was photographed in the same way as the pollen grains, and was then used to measure the diameter (plate 2). 1mm of the ruler was equal to 2.5µm, and pollen diameter was measured to the ½ mm. The total number of probes for the studied trees is presented in table 4.

Table 4: Probes of pollen from anthers

	probes	trees	within tree comparisons	pollen grains	average pollen/probe
F. excelsior	38	8	9	2052	54
A. pseudoplatanus	52	38	13	2468	48
T. cordata	23	8	9	952	42

Comparisons within trees included temporal and spatial comparisons, as well as pollen from male and hermaphrodite flowers in *F. excelsior* and *T. cordata*.

The pollen to ovule ratio at inflorescence level was calculated at "scale of magnitude" level using the most reliable values for pollen grains per anther (see introduction) and the male and female flower numbers that were observed.

Flower visitors

Insects in the inflorescences were studied by collecting whole inflorescences, cutting them with scissors and letting them fall directly into a vial filled with 70% ethanol. Attention was given not to disturb the twigs with the gondola prior to collection. 31 probes from 13 *A. pseudoplatanus* trees (typical probe size three inflorescence) and 16 probes from seven *T. cordata* trees (typical probe size 15 inflorescence) were collected in 2004. Inflorescences of *F. excelsior* and A. *platanoides* were occasionally collected but not systematically studied in this respect. Insects from *T. cordata* inflorescences were also collected in the same manner into a glass with ethyl acetate in 2005, to enable identification of chalcid wasps at species level. Also, gall midges and chalcid wasps were handpicked in 2005 using a small glass tube with a slap-on lid from buds into which they oviposited (plate 8).

Identification of chalcid wasps by Stefan Vidal (University of Göttingen), thrips by Laurence Mound (CSIRO, Australia), gall midges by Netta Dorchin (Bucknell University, Pennsylvania), true bugs by Albert Melber (University of veterinary medicine, Hannover), nitidulid beetles by Thomas Wagner (University of Koblenz).

Bees and flies visiting the inflorescences were not systematically recorded and identified because of methodological difficulties (impossibility of continuous observation during the whole flowering period with the crane, scarcity of them during flowering of *A. pseudoplatanus*). Visits of bees to *A. platanoides* inflorescences were video filmed and visit times were measured with a stopwatch, but these include only 39 visits in total.

Exclusion by covering inflorescences with nets of mesh 1mm and 0.2mm as well as paper bags (similar to Moog et al. 2002, plate 1) unfortunately failed due to alteration of phenology in *F. excelsior*, damage to bags, herbivore and fungal damage to the inflorescences within the bags (*Acer* spp., *T. cordata*), and the inability even of paper bags tightened to the twig with a cable tie to exclude thrips.

Parus caeruleus L. birds (blue tits, Blaumeisen) visiting inflorescences of *F. excelsior* and *A. platanoides* were video filmed, and their visiting times were measured (44 visits on three dates in 2004 on *F. excelsior*). Bird nets were hanged at different positions (between 20 and 30m height, within, above, below and between crowns) in crowns of *F. excelsior* (net height 2.5m, net width 2m, 3m, 6m, plate 1). In 2004 and 2005, each net was hanged in average three times per year for 4-5 hours each time. Hanging method: Three meter long canes were tightend vertically to twigs at carefully preselected locations at both planned edges of the net. The net was then connected to one cane with long cable ties and was streched to the other cane. Finally the cable ties were tightened and twigs were connected to branches behind them to increase the tension of the net. Pollen from about 1cm^2 from the head of the one bird caught was taken with a sticky tape (Dafni 1992), and pollen grains were counted under the microscope.

Infestation of *F. excelsior* by inflorescence galls (caused by *Aceria fraxinivora* Nalepa, Acari, Eriophydae, Buhr 1964, *A. fraxinivorous* in Castagnoli 1996) was classified as either slight (few galls, usually as part of intact infructescences) or heavy (usually on more than 1/3 of the twigs) as described by Wardle (1961). Gall weight on the trees was estimating in 2004 by sampling galls from 9 trees, weighing them (fresh and after an hour drying in 70°C) and dividing the weight by the fraction of sample size to total number of galls on each tree (facilitated by an estimation of twig number per tree on 38 trees, Tal 2003). These 9 trees were selected to represent the whole range of variation in total weight of galls and were used as a basis for a visual assessment of gall weight on other 18 trees, which were mostly slightly infested.

Pollination level

Pollen on stigmas and pollen tubes in styles were studied by collecting inflorescences in 70% ethanol, cutting out whole pistils in *F. excelsior* and styles with stigmas in *A. pseudoplatanus* and *T. cordata*, dying them with aniline blue (Martin 1959, 0.1M $K_3PO_4 \cdot 3H_2O$ and 1gr 0.1% aniline blue, filled to 1l with distilled water and mixed for two hours, kindly prepared by Monika Langlotz of the Heidelberg institute for plant sciences, Erbar et al. 2001) and observing pollen and pollen tubes using fluorescence microscopy (Dafni 1992). Pistils and styles with stigmas were slightly squashed to enable observation of pollen tubes within the tissues, and observed from one side only. Inflorescences were collected from treetop

arbitrarily, at constant locations during the season, and from different locations as comparisons. Sample sizes were from *F. excelsior* in 2002, 35 probes from 17 trees with total 417 pistils (further analysis of data from Tal 2003), from *T. cordata* in 2003, 24 probes from 8 trees with total 571 pistils, and from *A. pseudoplatanus* in 2004, 92 probes from 28 trees with total 1403 pistils (taken from the same probes in which insects were counted).

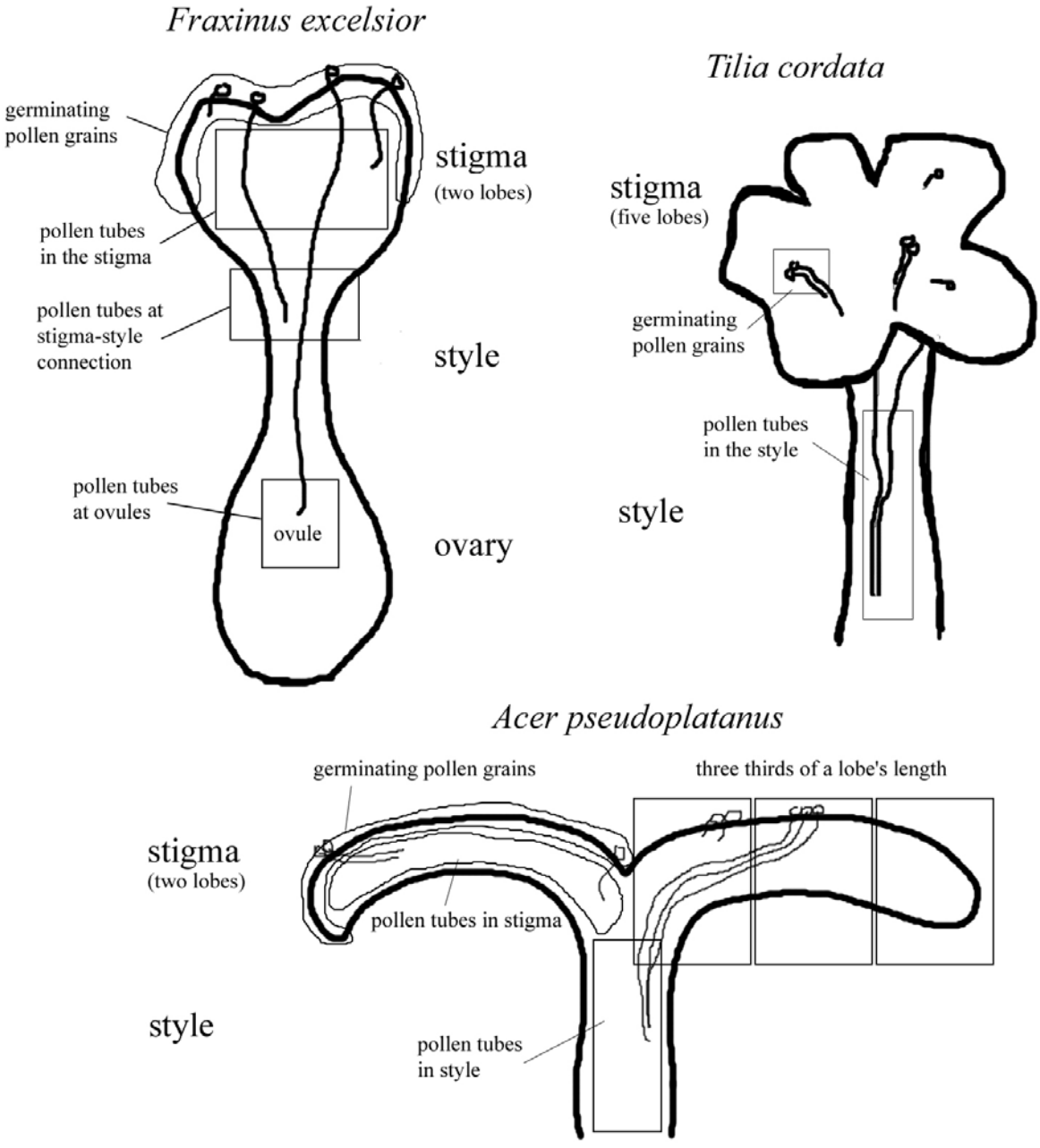


Figure 3. Pistils of *F. excelsior*, and styles with stigmas of *A. pseudoplatanus* and *T. cordata* with germinating pollen grains and pollen tubes. The outlined zones are the ones in which germinating pollen grains and pollen tubes were counted (four zones in *F. excelsior*, three zones in *A. pseudoplatanus*, two zones in *T. cordata*). Germinating pollen grains on stigma lobes of *A. pseudoplatanus* were additionally counted after their location in one of three thirds along the lobe. Groups of germinating pollen grains in *A. pseudoplatanus* and *T. cordata* are also shown and were counted. The drawings are after photos, but not in a common scale.

For each pistil the number of germinating pollen grains and the number of pollen tubes in different locations was counted (see figure 3). In *A. pseudoplatanus* and *T. cordata* the number of size of groups of germinating pollen grain was recorded. A group was defined to be all pollen grains that were less than two pollen diameters apart. In *A. pseudoplatanus* the pollen grains on each stigma were also counted in respect to their location along the stigma, as belonging to one of the three parts: outer, middle or inner third of each lobe's length (figure 3). This was assessed in 42 of the probes. In *T. cordata* comparisons were made of probes from different heights in a tree and between flowers at different stages of anthesis (anthers closed or opened and corolla white or yellow - beginning and ending of female anthesis, respectively). The probes of *T. cordata* are from the first half of the flowering season in the stand, but include trees at the end of their anthesis.

Fruit

Fruits were collected in the second half of September, after aborted fruit has fallen, but before ripe fruit began to fall (Gardner 1977, Hong and Ellis 1990, Götz and Wolf 2004), from crown tops. All samples were counted, and fruit was checked for seeds. Assessments of total fruit per tree were done in a multiplicative manner, after the assessment of the number of twigs in *F. excelsior* (see details in Tal 2003), number of infructescences in *Acer* spp. and the number of sample areas included in the total crown envelope in *T. cordata*. Some of the assessments were checked at different dates or from different view angles in order to assess the estimation error, which is 30-50%. Further details for the species:

1. *F. excelsior* – Fruit on 19 large canopy trees were counted in 2002-2005 (the median probe size was 450 fruit). Fresh and dry weights were measured before and after drying in 70°C for an hour (2004, samples from 13 trees). The number of fruit from exposed and covered twigs were compared just after flowering (not ripe fruit). In 2004 this comparison was done on eight trees, in median 5 twigs (range 3-11) with median 13 infructescences (range 8-40) each.
2. *A. platanoides* – Samples were collected and fruit was checked for seeds as described for *A. pseudoplatanus* below. The four large trees fruiting in 2004 were sampled, overall 283 infructescences with 1152 fruit were collected. The results include samples from all heights in the crown.

1. *A. pseudoplatanus* – Each sample was a complete collection from three branches, and included large and small infructescences. Sample sizes were 58 probes from 44 trees

in 2004, average 35 infructescences per tree (from all trees more than 20, total 1761 infructescences with 16931 fruit), in 10 trees comparisons within the crown were made, the results include only probes from treetop. The procedure was replicated in 2005 with 40 probes from 40 trees in 2005 (total 1320 infructescences with 10749 fruit). 121 fruit of 5 trees in 2004 were dried at 70°C for an hour and weighed at parts (carpel, wing, seed) in respect to their belonging to a fruit having 2,1 or no seeds. In all samples the range of wing lengths (one mericarp) and the range of angles between the tangents of the straight part of the mericarp wings were measured for fruit containing two seeds (accuracy ½ cm and 10° respectively). The ranges were compared between 2004 and 2005 for 16 trees. The seed per fruit ratio was calculated as the median of seed per fruit ratios from all infructescences in the sample (i.e. fruit with three mericarps included).

3. *T. cordata* – Each sample included all infructescences of a whole branch system in the upper crown, covering a partial area of the crown envelope. Sample sizes were 33 trees in 2004 (3489 infructescences, 10247 fruit) and 9 trees in 2005 (590 infructescences, 879 fruit), including comparisons from different heights in the crown. A comparison of fruit from covered and exposed inflorescences was made on 11 trees, one in two heights, total 143 covered, 332 exposed inflorescences. Covers that were found to be torn or punctured were left out.

Results

Overview

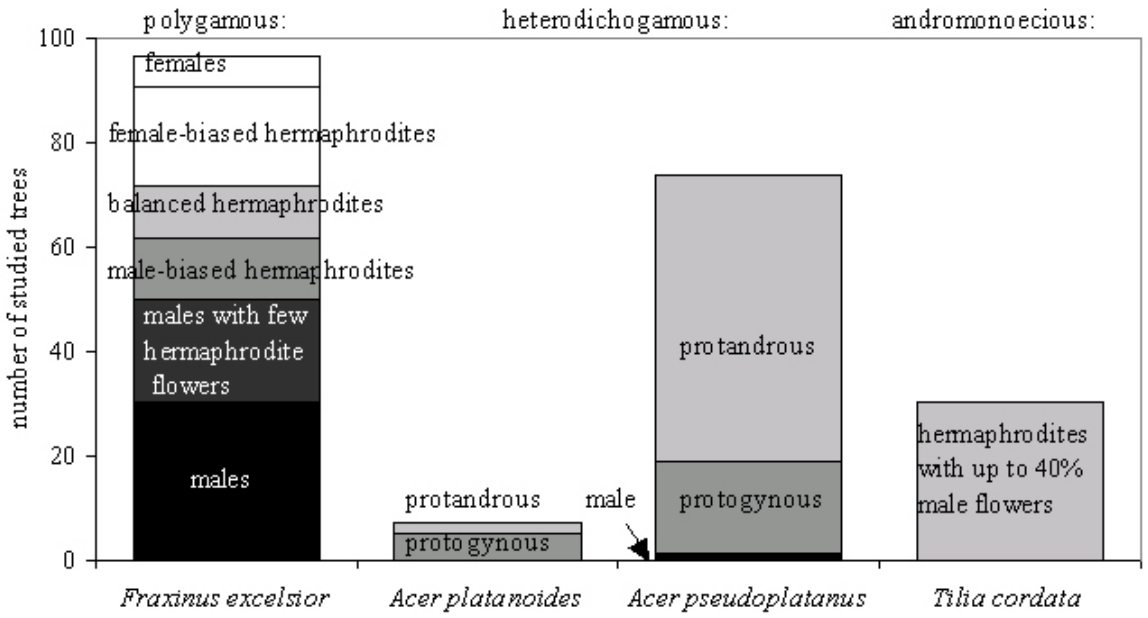
The sexual systems of all four species had proved to include different grades of gender separation (figure 4a). In *Fraxinus excelsior* tree types were characterized by morphological flower gender, in *Acer* spp. by temporal patterns of gender expression and in *Tilia cordata* an initial grade of gender separation, that of andromonoecy, was found. Male gender was found to dominate in all species – in tree number in *F. excelsior*, flower number in *Acer* spp. (figure 22) and in flower gender in *T. cordata* (figure 28, table 19).

The pollen to ovule ratios at inflorescence level per individual tree ranged in *F. excelsior* practically from 0 to ∞ (figure 4b), depending on tree gender, and was different in *A. pseudoplatanus* between protogynous and protandrous trees, as they had a similar number of male flowers, but the former had less female flowers per inflorescence (figure 22). *A. platanoides* had lower ratios than *A. pseudoplatanus* mainly due to a lower male to female flower ratio in the inflorescence (Semm 1966), and the pollen to ovule ratio at inflorescence level in *T. cordata* varied according to different proportions of male flowers in different trees. Flower number in the largest trees reached 4-5 million in *F. excelsior*, ½-2 million in *T. cordata*, ⅓ to ½ million in *A. pseudoplatanus*, and 50-100,000 in *A. platanoides*.

The species flowered consequently and mostly non-overlapping (*F. excelsior* and *A. platanoides* overlapped in one to two weeks of their main flowering period, the two *Acer* species did not overlap). Leaves unfolded in the canopy from the end of April to mid May, flowering *A. platanoides* were among the first trees to flush and *A. pseudoplatanus* flowered just after their leaves unfolded (table 5).

Flowering intensity was high and constant in *F. excelsior*, whereas in *Acer* spp. and *T. cordata* it fluctuated between study years (figure 5). In the former the flowering intensity of individual trees (hermaphrodite and female) fluctuated, but was buffered by the constant full flowering of male trees and the asynchrony of non-flowering years. Flowering duration fluctuated in early flowering *F. excelsior* more than it did in the later flowering species (table 5).

a:



b:

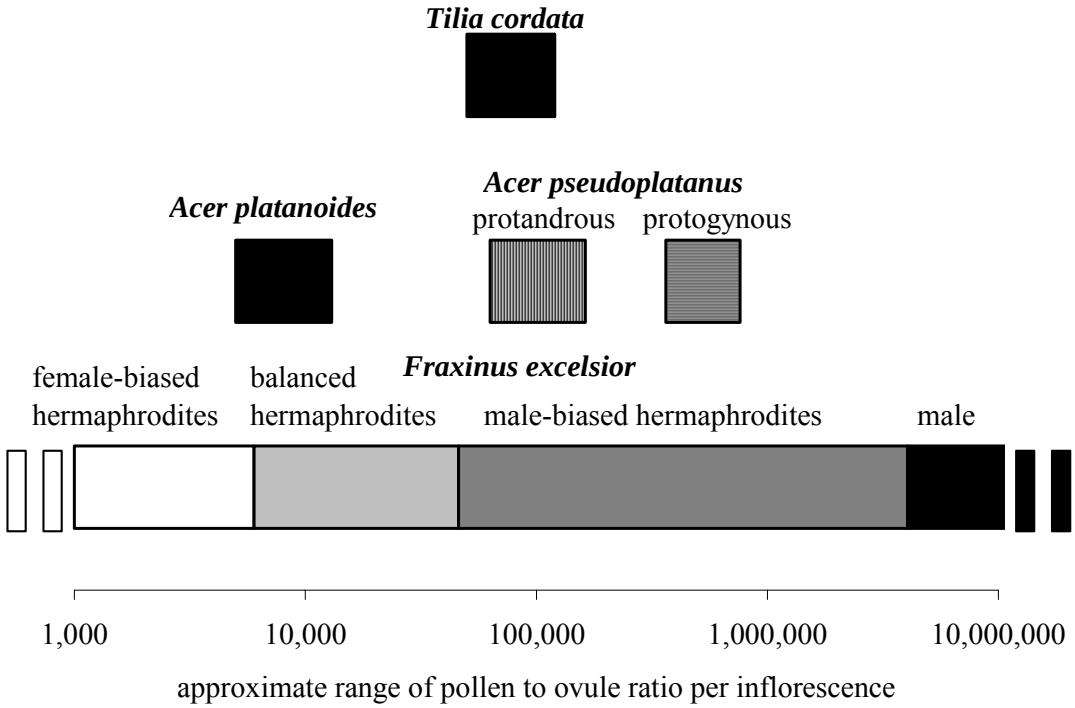


Figure 4: Gender type distribution (**a**) and pollen to ovule ratio at inflorescence level (**b**) in the studied species in the stand.

Table 5: Flowering period of the studied trees in the stand and its duration in weeks (rounded to full weeks). Main flowering period is in bold typeface, overall flowering period in parentheses.

Species	flowering time, relative to flushing		2003	2004	2005
F. excelsior	mid March - mid April	before	**2** (4)	**3** (6)	**2** (3)
A. platanoides	mid to end April	together	(2)	**2** (3)	-
A. pseudoplatanus	end April - end May	just after	(4)	**4** (5)	**3** (5)
T. cordata	mid June - mid July	long after	ca. **3** (5)	ca. **3** (5)	**2** (3)
* In 2002 *F. excelsior* flowered **5** (8) weeks (Tal 2003), in 2006 *F. excelsior* and *A. platanoides* flowered **2** (3) weeks in the second half of April.					

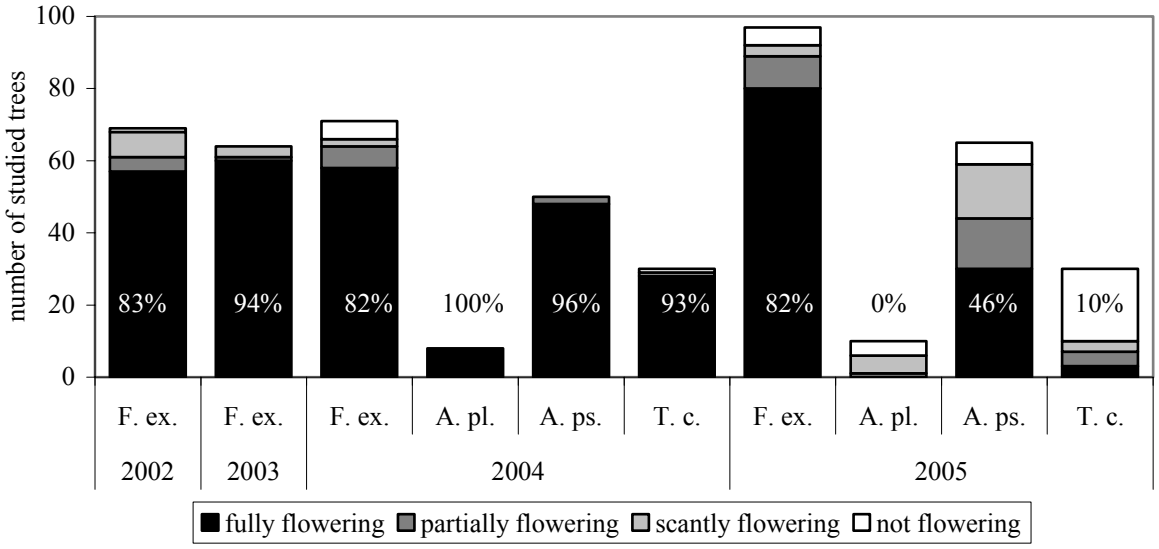


Figure 5: Flowering intensity of the tree species in the stand. The numbers denote the proportion of fully flowering trees from the number of studied trees in each year. Abbreviations: F. ex. = *Fraxinus excelsior*, A. pl. = *Acer platanoides*, A. ps. = *Acer pseudoplatanus*, T. c. = *Tilia cordata*.

F. excelsior had more stigmas with germinating pollen grains than *A. pseudoplatanus* and *T. cordata* (87% versus 42% and 51%, respectively), and more germinating pollen on these stigmas (medians 10 versus 4 and 5, respectively). In *A. pseudoplatanus* an evident difference was found between protogynous and protandrous trees (58% and 5 versus 26% and 3, respectively). The number of pollen tubes was significantly correlated with the number of germinating pollen grains in all the species. The slope of the regression between the number of germinating pollen grains and the number of pollen tubes in the style was 100-150:1 in *F. exscelsior*, 30:1 in *A. pseudoplatanus* and 3:1 in *T. cordata*.

The pollination modes could not be directly studied. The apparent pollination agents were wind in *F. excelsior*, solitary bees in *A. platanoides* (*Andrena* cf. *haemorrhoa*), thrips (*Taeniothrips inconsequens*) in *A. pseudoplatanus* and *Bombus* spp. in *T. cordata*. Wind might have played a role in the latter two species as well.

Thrips were the most common insects in the inflorescences (*Taeniothrips inconsequens* in *F. excelsior* and *Acer* spp., *Thrips major* in *T. cordata*). The abundance of adult thrips in the inflorescences of *A. pseudoplatanus* was high only in the beginning of the flowering season, and was significantly correlated with pollen loads on the stigmas.

Fruit production followed in its extent the flowering intensity and was the highest and most constant in *F. excelsior*, followed by *T. cordata* (figure 6). Most yield in both species was produced by the few largest trees. *A. pseudoplatanus* produced much less fruit than the former two species. It also produced markedly less seeds than fruit, especially in protandrous trees and in 2005, and its yield was also more spread among individual trees.

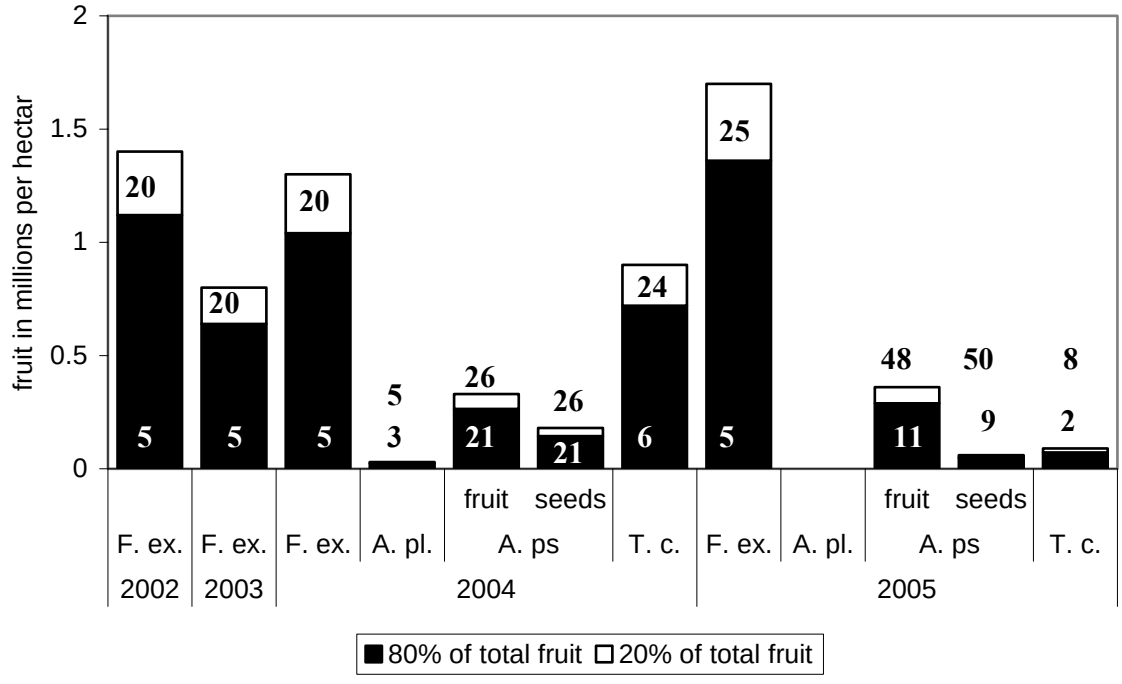


Figure 6: Fruit production per species in the study years. The yield is separated to 80% and 20% parts (black and white respectively). The lower number denotes the number of largest trees producing the 80% part and the upper number the trees producing the rest 20%. Seed production is shown for *A. pseudoplatanus* (in *F. excelsior* and *T. cordata* it equaled approximately the fruit number). Abbreviations: F. ex. = *Fraxinus excelsior*, A. pl. = *Acer platanoides*, A. ps. = *Acer pseudoplatanus*, T. c. = *Tilia cordata*.

Fraxinus excelsior

Gender

A half of the *Fraxinus excelsior* trees in the stand were purely male (or had very few hermaphrodite flowers). The other half ranged from predominantly male to purely female trees. About a quarter of the trees were predominantly female (figure 7a).

Some trees changed gender categories between years. In respect to 2002, eight trees in 2003 and 15 trees in 2004 were assigned a different gender. All the changes but one were between the neighbouring categories male and male with few hermaphrodite flowers (seven in 2003 and eight in 2004, in respect to 2002) and male biased hermaphrodites and balanced hermaphrodites (one in 2003 and six in 2004, in respect to 2002). Taking a change towards a more female category as +1 and towards a less female category as –1, the sum of changes had the same tendency as the average minimal temperature at the beginning of flowering (figure 7b, Pearson product moment coefficient 0.99 p=0.08). In several instances the usually feeble pistils of hermaphrodite flowers on predominantly male trees were observed to wither at the beginning of their anthesis by cold weather.

Within the buds, a larger variety of flower forms was found than in the unfolded inflorescences. Hermaphrodite embryonic flowers (1mm long) were found in both purely female and purely male trees, and stamens and pistils were of more similar sizes in embryonic flowers than they were in mature flowers of biased hermaphrodites. Apical flowers in the inflorescence tended more to a hermaphrodite morphology than the common flower form in the inflorescence, which was especially evident in male-biased hermaphrodites and balanced hermaphrodites. Basal flowers were often female in female-biased hermaphrodites.

A clear distinction could be made between male and male-biased hermaphrodites on the one hand, and balanced hermaphrodites, female-biased hermaphrodites and females on the other hand. In the following these groups are referred to as males and hermaphrodites/females respectively. Males differed from hermaphrodites/females in tree size, twig morphology, gall infestation, flowering intensity and frequency, inflorescence phenology and fruit production, as presented below.

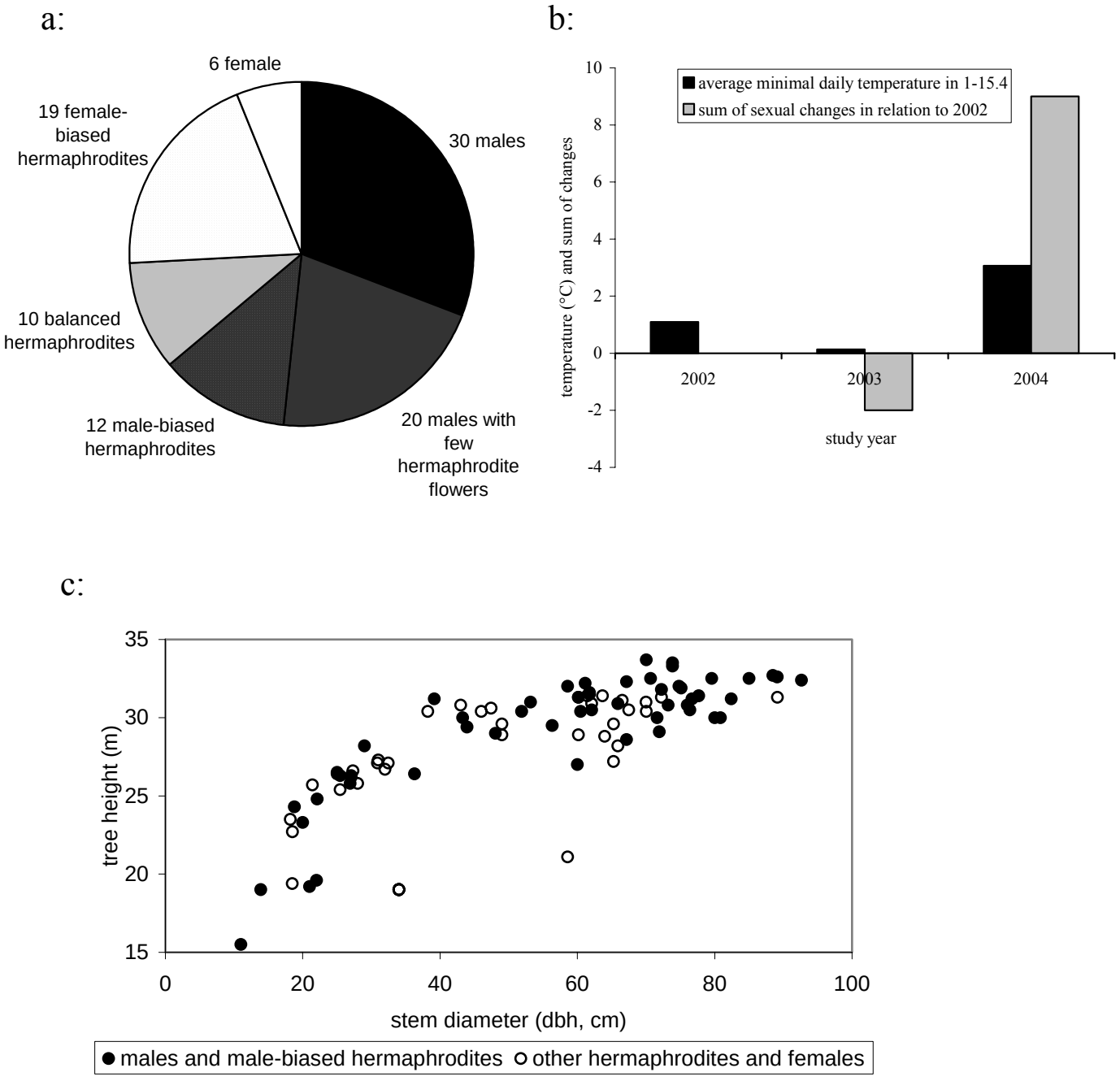


Figure 7: *Fraxinus excelsior* – tree gender. **a**: Gender distribution of 97 trees in the stand. **b**: Sums of number of changes between categories of tree gender in 2003 and 2004 in relation to 2002 (a change to a more female category was taken as +1, a change to a less female category was taken as -1) and the average minimal daily temperature in the first half of April, which was the main flowering time, figure 11. **c**: Gender and tree size. Tree height and stem diameter of canopy *F. excelsior* trees separated after the two main groups: Males (and male-biased hermaphrodites) versus hermaphrodites/females.

Large male trees were significantly larger than large hermaphrodite/female trees (figure 7c, stem diameter of males 68.9±12.0cm (average±standard deviation) versus hermaphrodites/females 61.8±10.9cm, t test p=0.03, tree height of males 31.2±1.3m versus hermaphrodites/females 30.3±1.0m, Mann-Whitney rank sum test p=0.007, these data are for trees with stem diameter above 40cm and tree height above 28m, being 68% of all canopy trees). However, taking all canopy trees the gender groups did not significantly differ in size (Mann-Whitney rank sum test p=0.22 for stem diameter, p=0.10 for tree height). Male trees had thicker twigs, larger inflorescence buds and more buds per twig than hermaphrodites/females.

The median of pollen grain diameter for all probes from fresh dehisced anthers was 22.5µ, the 1st and 3rd quartiles were 20µ and 23.75µ respectively. Considering the measurement error the result may be expressed as 22±2µ. Individual trees varied significantly in their pollen diameter (Kruskal-Wallis one way analysis of variance on ranks $p<0.001$), the medians per tree ranged 17.5µ-26.25µ, 10 of 23 trees had the median 22.5µ. Males and hermaphrodites/females did not differ significantly in pollen diameter (Mann-Whitney rank sum test p=0.4), but conspicuously the four trees with largest pollen (≥25µ) were all hermaphrodite (female-biased and balanced). On male-biased hermaphrodite trees, the pollen from the male flowers and from the hermaphrodite flowers differed significantly in diameter but not in a consistent direction.

Massive gall infestation was found only on males (plate 8). Total gall weights were 13.5kg and 10kg for the heaviest loaded trees, further 4, 5 and 8 trees bore around 5kg, 2kg and 1kg respectively (air dried weight). Other nine trees, including six hermaphrodites/females, had only a few galls per tree (ca. 100gr). The intensity of gall infestation changed on some trees between years, but was not quantitatively recorded.

Males flowered every year in a full intensity, whereas hermaphrodites/females skipped intensive flowering every two to three years (figure 8). Inflorescences on males unfolded from large buds and had a "waiting phase" in which anthers were exposed but stayed closed for one to two weeks and then opened from the southern aspect of the spherical inflorescence (plate 3). Inflorescences on hermaphrodites/females were elongated and unfolded gradually from smaller buds, exposing the stigmas gradually. See details and implications of this difference in the phenology section.

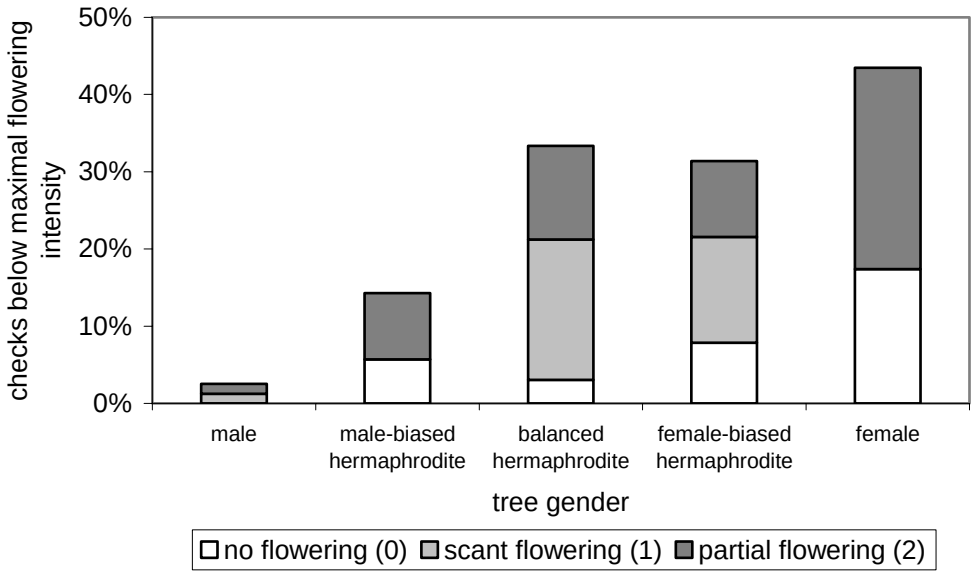


Figure 8: The frequency of flowering below maximal intensity as percent from the total number of checks (all years together, see figure 10) after gender.

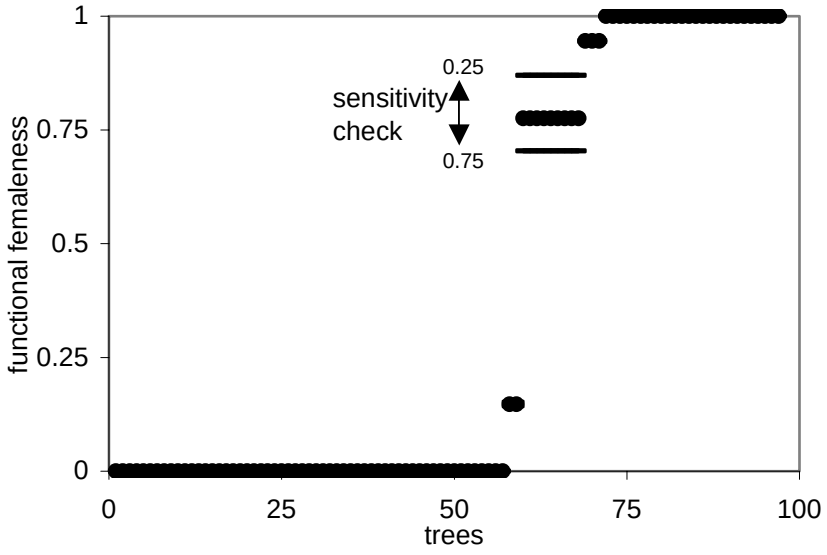


Figure 9: Functional femaleness for trees after gender groups, calculated under the assumptions in text. The sensitivity check refers to the assumption of 0.5 maleness of balanced hermaphrodite, the resulting values for assuming 0.25 and 0.75 are shown. Trees sorted after their relative rank.

Functional gender was assigned to the trees more or less groupwise using the following assumptions for female and male functions, based on the morphological and phenological results (figures 8 and 10, table 7, plates 2 and 3) as well as on the findings to fruit production (figure 16a):

1. Balanced hermaphrodites and female-biased hermaphrodites have a full female function (1).
2. Males and male-biased hermaphrodites have a full male function (1).
3. Female-biased hermaphrodites have a low male function and male-biased hermaphrodites have a low female function (both in the range 0-0.1, tree specific assigned, depending on anther size and fruit set).
4. Balanced hermaphrodites have a partial male function (0.5, ±0.25 as a sensitivity check).

For each tree femaleness was calculated after Lloyd (1980) as F / (F+M·E), with F and M its female and male function respectively and E the sum of female functions divided by the sum of male functions (E=0.58). The resulting composition of the population is bimodal (figure 9). Tree height is negatively and significantly correlated with the femaleness (Spearman rank order coefficient –0.31, p=0.0023).

Flowering phenology

Fraxinus excelsior flowered in the stand in a more or less constant overall intensity of 80% of the trees in full intensity over the four study years (figure 5, the other trees usually flowered partially). The flowering intensities of the individual trees are presented in figure 10. The average intensity of flowering was 2.7 (±0.7 standard deviation). The variation between years was small (2.9±0.4 in 2003 vs. 2.7±0.9 in 2004 were the extremes), and the correlation with gender was significant (figure 8). The average intensities were for males 3.0±0.3, male-biased hermaphrodites 2.7±0.7, balanced hermaphrodites 2.4±0.9, female-biased hermaphrodites 2.4±1.0 and females 2.2±1.1. Significant statistical differences were found between male trees and hermaphrodite, female-biased hermaphrodites and females (Mann-Whitney rank sum test, p=0.005, 0.002, 0.001 respectively) but not between males and male-biased hermaphrodites (p=0.27), male-hermaphrodites and female (but almost, p=0.06), nor in other comparisons.

2002, male: 333313333313___333_3__333_333333____3333333_333__3
2003, male: 333___333____33333_3__333333333333__3333333_333__3
2004, male: 333332333__3333333333333__333333____3333333_3_3__3
2005, male: 333233333333333333333333333333333333333333333333333333

2002, mh: 33_32__3333_ h: 313__31313 fh: 333_1___333133____3 f: 223302
2003, mh: 33_333_333__ h: __3__33331 fh: 333_13__333____3__1 f: 3_2333
2004, mh: 333_2__333__ h: 3_30333313 fh: 203_23__3_3210____3 f: 302033
2005, mh: 030333233333 h: 3223323132 fh: 2300333313132333333 f: 233303

Figure 10: Flowering intensities of 97 *F. excelsior* in 2002 to 2005. Each tree corresponds to a column of four digits, denoting: 3 = fully flowering, 2 = partly flowering, 1 = scanty flowering, 0 = not flowering, _ = not studied in this year. The trees are grouped after gender: mh = male-biased hermaphrodites, h = balanced hermaphrodites, fh = female-biased hermaphrodites, f = females.

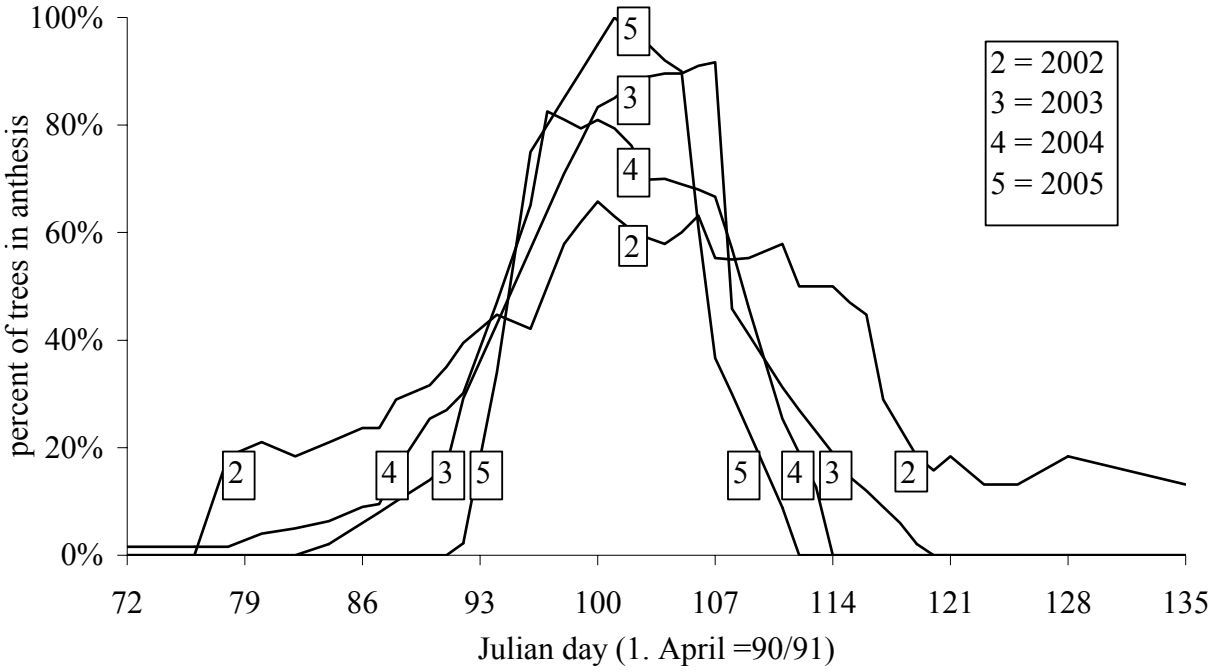


Figure 11: Flowering phenology of *F. excelsior* in the stand – an overview. The proportion of flowering trees is depicted after Julian date in the four study years (denoted by their last digit).

The period of flowering, represented by the number of flowering trees (figure 11), changed in duration between the study years. Whereas in 2002 it was spread over eight weeks (10%-90%) and included at its peak only 60% of all trees flowering together, the flowering in 2005 was short (three weeks) and intensive (all trees flowering simultaneously at peak flowering). However, the period in which over 50% of the trees flowered was quite constant in the study years between the 95th and the 108th Julian days, the first half of April (except for a 2-3 days delay in 2002). The accumulation rate of the percent of trees coming into flowering noticeably contrasted 2002 with 15% per week with 2005 with 90% per week (in 2003 and 2004 the value was intermediate – ca. 50% per week).

Phenological diagrams of the trees in the stand revealed more details on the differences between the years (figure 12):

1. In 2002 the flowering started early and ended late, the individual trees flowered gradually and long. The overlap among trees was low, especially among female flowering trees that could be almost separated temporally to small groups during flowering season (Tal 2003).
2. In 2003 flowering was interrupted by a cold week, causing frost damage in all tree flowering (figure 12, figure 43 in appendix, plate 4) and postponing the anthesis of trees that had not yet flowered.
3. In 2004 one tree began flowering long before the rest (this happened also in 2002 and 2003, but is less conspicuous in the diagram), and the flowering of most other trees was within a short period.
4. Even more so in 2005, which contrasts 2002 most strongly in the intensive and brief flowering of the stand. All trees flowered almost synchronously (notice the time axis in relation to the other years).

This variance was related to climatic factors, mainly to the date of the end of winter (last long cold period) and to the number of cold periods in April, as analysed in the appendix (table 29). The phenology diagram of 2003 is somewhat schematic due to a cold week (2-10.4) that damaged the flowers and interrupted the checks. The diagram of 2005 is somewhat coarse as stand surveys were not frequent enough to follow the rapid anthesis in a higher resolution. 2006 is not included in the study, but as it was a year with an exceptionally late winter end (in the very end of March, see appendix), it is noted that *F. excelsior* main flowering time was in the second half of April (approximately 13-26.4).

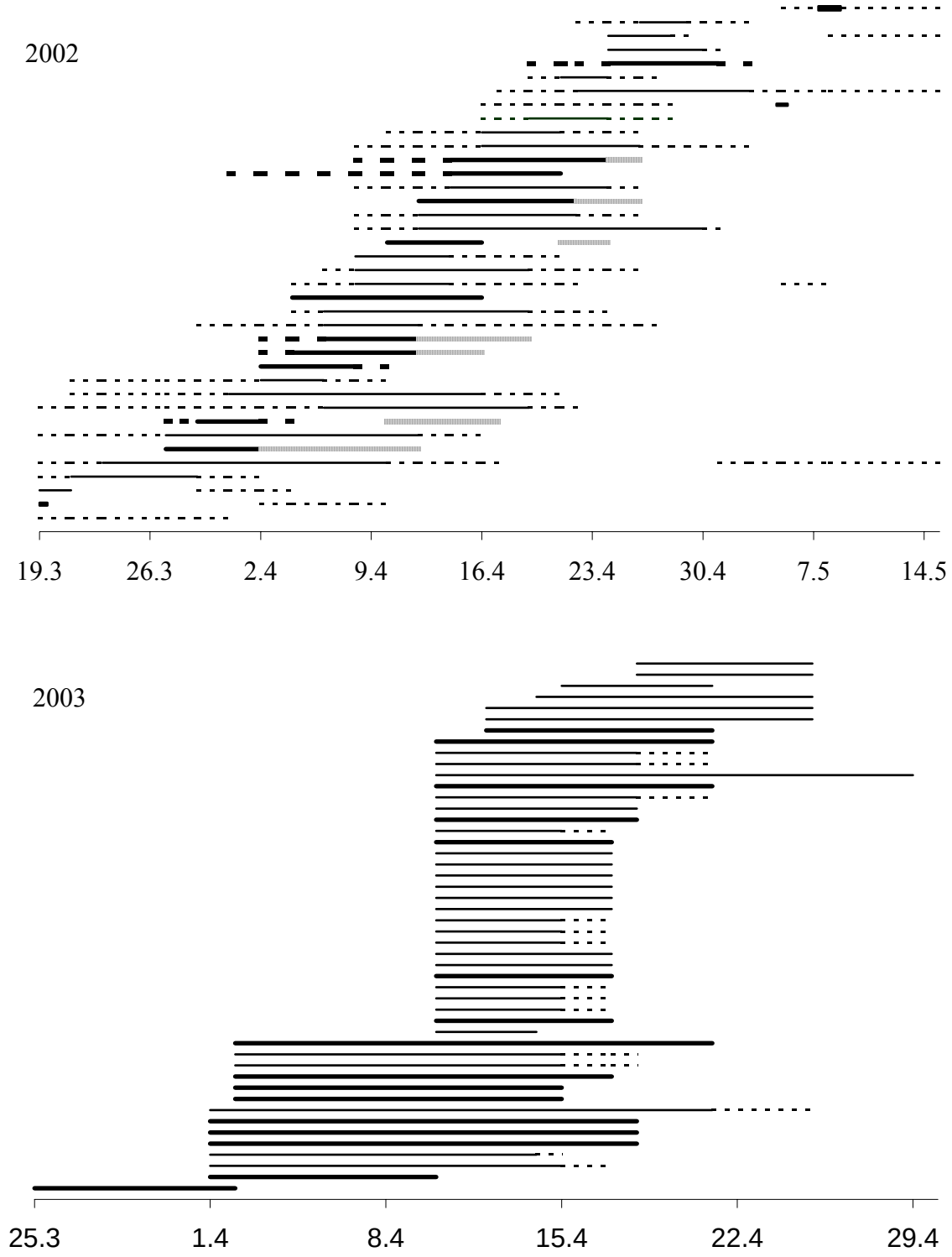


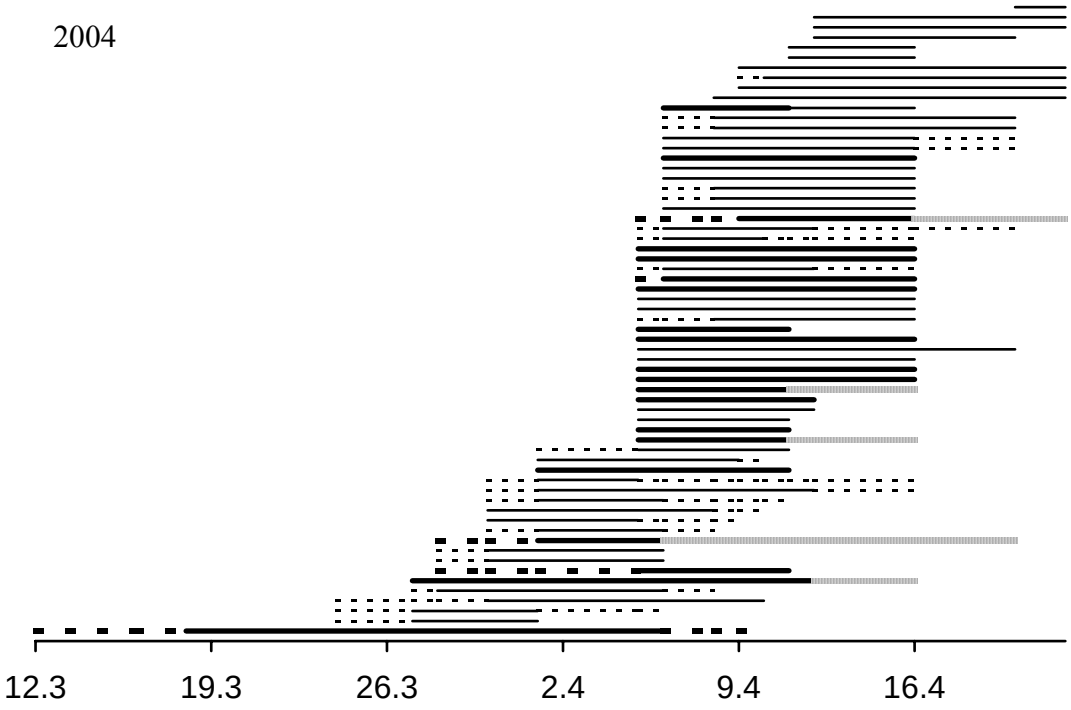
Figure 12: Flowering phenology of *F. excelsior* in the stand – detailed view. The years 2002 through 2005 (38, 48, 63 and 90 trees respectively) are presented separately, line types after the legend:

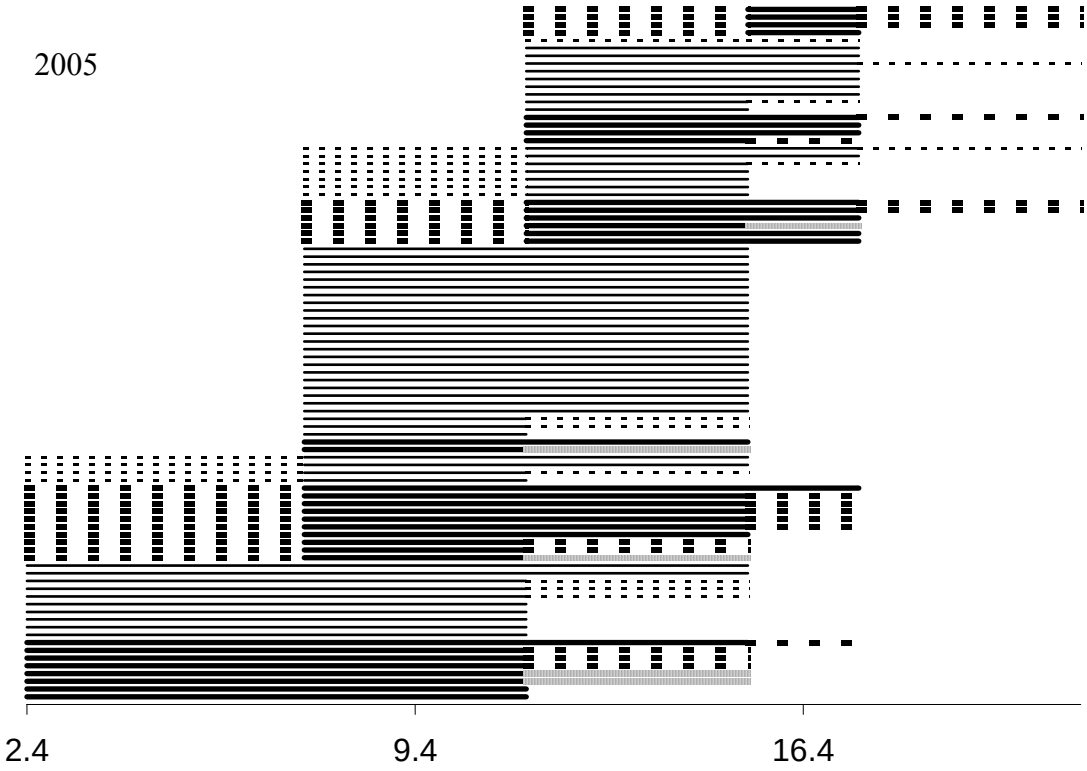
male — total anthesis — female

main (10-90% of tree)

residual (0-10% or >90%)

male flowering of hermaphrodite trees


2004
12.3
19.3
26.3
2.4
9.4
16.4


2005
2.4
9.4
16.4

The median duration of flowering per tree was 16 days in 2002, 11 days in 2004, 9 days in 2005 and 8 days in 2003 (Mann-Whitney rank sum tests: 2002 vs. others $p<0.001$, 2004 vs. 2005 $p=0.002$, 2004 vs. 2003 $p=0.06$, 2003 and 2005 did not differ significantly $p=0.7$). The dates for individual trees of the beginning and end of flowering were significantly correlated in all study years. Still, early flowering trees usually flowered longer - the duration of flowering was in three of four years correlated negatively and significantly with the starting date, (a week later resulted in 2-5 days shorter flowering, the extremes were for 2002 and 2005 respectively). In 2004 the duration of flowering was not correlated with the starting date but with the end date of flowering (later ending was longer flowering). Table 6 presents these correlations as Spearman rank order coefficients and as regressions for the significantly correlated parameters. The start and end dates of flowering correlated positively and significantly for all study years, with regression coefficients between 0.4 and 0.8 (i.e. a tree starting to flower 5 days later, ends the flowering between 2 and 4 days later). This correlation was stronger in gradual 2002 than in the condensed 2005.

Table 6: Correlation of the total duration of anthesis, starting and end date of anthesis for all trees as Spearman rank order coefficients and as regressions of the significantly correlated parameters. Dates are expressed as days since the beginning of flowering, denoted by "start" in the first column. Abbreviations: D = Duration, S = starting date, E = end date.

year (start)	Duration and Start		End and Start		End and Duration	
	coef.	regression	coef.	regression	coef.	regression
2002 (19.3)	-0.4*	D=20.4-0.24S (p slope=0.02)	0.86	E=20.4+0.76S	ns (p=0.98)	
2003 (25.3)	-0.57	D=17.8-0.53S	0.44*	E=17.8+0.47S	0.38*	E=21.1+0.32D (p slope=0.02)
2004 (12.3)	ns (p=0.37)		0.75	E=21.0+0.58S	0.48	E=29.2+0.53D
2005 (2.4)	-0.73	D=12.6-0.68S	0.53	E=12.2+0.37S	ns (p=0.36)	
For all coefficients $p\leq0.001$, except * $p\leq0.01$, ns =not significant.						

Male and female flowering did not differ significantly in the duration of main flowering, which was about a week in all years (table 7, Mann-Whitney rank sum test $p=0.6$ to 0.9, the same test is applied below). They however did differ significantly in the duration of overall flowering in 2005 ($p<0.001$) and 2003 ($p=0.04$), female flowering being longer (in 2002 the difference was not significant, $p=0.08$). The male phase of balanced hermaphrodites was

significantly shorter than the flowering of males ($p<0.001$ in 2005 and 2002, $p=0.013$ in 2004). The overall flowering of balanced hermaphrodites was longer than the overall flowering of female-biased hermaphrodites and females (in 2005 $p=0.04$ and 2002 $p=0.012$, but not in 2004, $p=0.15$), but their female flowering was shorter (in main and overall flowering in median one and two days respectively, with p's 0.16 and 0.3, not statistically significant).

Table 7: The median duration (in parentheses - average duration ± standard deviation) of main and overall, male and female flowering. See statistical tests in the text.

year/gender	male		female		male phase of balanced hermaphrodites
	main flowering	overall duration	main flowering	overall duration	
2002	6 (7.7±5.6)	18 (16.8±8.9)	6 (6.9±1.8)	10 (12.0±3.9)	4 (4.8±2.7)
2003	7 (8.6±4.1)	7 (9.8±4.5)	not checked	11 (11.8±4.2)	not checked
2004	8 (8.5±3.1)	11 (11.0±3.2)	10 (9.2±3.8)	11 (11.0±5.3)	5.5 (6.7±3.7)
2005	8 (7.0±2.3)	8 (8.6±2.3)	6 (6.5±2.7)	13 (11.4±3.0)	4 (3.6±0.9)

Female flowering started before male flowering in 2003 (eight days in median, $p=0.013$), but not in the other years (2004 and 2005 $p=0.14$, 2002 $p=0.9$). Female flowering ended after male flowering in 2005 (two days in median, $p<0.001$), but not in the other years (in 2002 and 2004 males were later, $p=0.06$ and $p=0.08$, respectively, in 2003 $p=0.35$).

The durations of flowering for individual trees were significantly correlated between 2002 and 2004 (Spearman rank order coefficient 0.35, $p=0.03$). The flowering durations in the other pairs of years did not correlate significantly (p's between 0.25 and 0.98).

The ranking of the trees was correlated significantly between 2002 and 2004 (Spearman rank order coefficient 0.73, $p<0.001$) and between 2005 and each of the years 2002, 2003 and 2004 (Spearman rank order coefficients 0.46, $p=0.005$; 0.42, $p=0.005$ and 0.54 $p<0.001$ respectively), but not between 2003 and 2004 nor between 2003 and 2002 ($p=0.3$, $p=0.8$,

respectively). The average duration of total flowering was negatively and significantly correlated with the average normalized rank of the trees (Spearman rank order coefficient -0.49, $p<0.001$), and the regression was: Average total duration = 14 - 6.9 · Average normalized rank (p for slope and coefficient <0.001), that is, coarsely stated, the first trees flowered two weeks, the last trees flowered one week. The correlations between average duration and tree rank for single years were 2002: -0.26 ($p=0.11$), 2003: -0.06 ($p=0.74$), 2004: -0.22 ($p=0.10$), 2005: -0.57 ($p<0.001$), i.e. early flowering trees flowered longer, as shown above. In 2002 early flowering male trees flowered longer than late flowering male trees whereas the duration of the female phase did not change during the season.

Synchrony among the trees in 2002 was low, in fact only 2-4 trees were female simultaneously and flowered parallel to only a few male trees (figure 12). Synchrony was high in the condensed flowering year 2005, almost all trees in the stand flowered simultaneous flowering of (figure 12, the changes on 11.4 are artefacts of temporal resolution). The synchronicity index and the step present these characteristics of the flowering phenology diagrams quantitatively (figure 13):

1. The flowering of *F. excelsior* was stronger synchronised in 2003 to 2005 than in 2002. Steps of 1-3% in the former are contrasted with steps of 6-12% in the latter. 2005 was the year of most synchronised flowering.
2. Synchronisation of the main flowering stages was somewhat stronger than of the overall flowering. Looking at the step, in 2002 the difference is large, in the other years negligible.
3. Trees of reciprocal gender were about as synchronised as trees of the same gender.

The measure - average duration of flowering divided by the standard deviation of starting dates - was for the overall duration in 2002-2005: 1.3, 2.0, 2.0, 2.9 respectively, i.e. it separated stronger 2005 from 2003 and 2004, and for the main duration it was 0.64, 1.9, 1.7, 1.9 respectively. Augspurger (1983)'s modified synchronicity index (see methods) was 15-25% lower than the synchronicity index and Albert et al. (2001)'s index was still 15-30% smaller, both preserved the order of the comparisons.

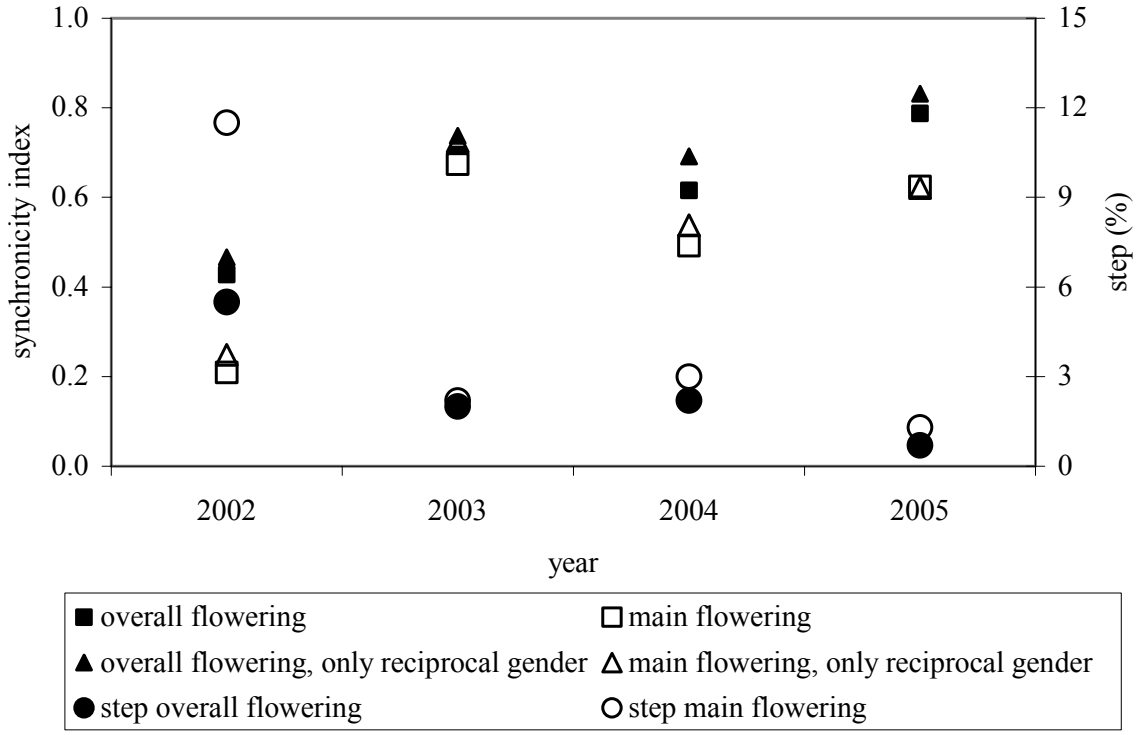


Figure 13: Synchronicity indices and steps for *F. excelsior* in the four study years, for the overall and the main flowering, and for all trees and only trees of reciprocal gender.

Within the crowns, the predominant pattern of flowering was from lower crown upwards and from inner crown outwards. This pattern was most evident in the upper meter of crown top in which both tendencies coincided. This pattern was most conspicuous in 2002, in which it was described quantitatively (Tal 2003), and clear but less pronounced in the following years as flowering phenology was rusher. This was the only phenological pattern consistently observed at crown scale. One tree had differences between western and eastern crown halves in three out of four years, in which the former flowered much earlier than the latter, and two trees flowered in only one half of the crown in 2004 and 2005. Unfolding of the leaves happened in 20 of 80 trees with a similar vertical pattern (lower crown further developed than upper crown), that was best observed at the initial stages, before the leaves hanged down. I could not find a connection between the flowering or not flowering of a tree in 2005 and the time its leaves unfolded.

Inflorescence phenology with its gradual unfolding of anthesis was responsible for much of the graduation of flowering in the tree. Inflorescence flowering patterns were gender specific (figure 14, plate 3):

1. Male inflorescences unfolded from large round buds (ca. 1cm wide) to a "purple knob" stage ca. 2 cm across, in which the closed anthers formed a compact sphere. In this state they stayed unchanged for two weeks in 2002 and 2003 and for one week in 2004 and 2005. Only after this "waiting phase" the anthers began to dehisce, usually without much lengthening of the inflorescence. The opened anthers formed a sector of the sphere, which gradually became wider till it spread over the entire surface. The centers of the flowering sectors deviated significantly from the middle axis of the inflorescence southwards (figure 14c, χ^2=54.2 with 14 df, $p<0.001$), and north facing inflorescences were the last to flower (65% of non flowering inflorescences were between NW and NO, the average direction of non flowering inflorescence was 187° with 0° as south; north facing inflorescences started flowering from one edge of the sphere, or sometimes from both edges and ended at the center!). Male-biased inflorescences unfolded in a similar manner, presenting the relatively feeble stigmas above the "anther sphere" during the waiting phase of the male inflorescences on the tree.
2. Balanced hermaphrodite inflorescences unfolded gradually, exposing more and more stigmas as they elongated (figure 14a). Inflorescences with relatively large anthers were quite spherical at the beginning of their unfolding, and relatively many stigmas were exposed from the beginning of unfolding, but these were still dark and not receptive. As the inflorescence lengthened the stigmas became lighter in color, swollen and fully receptive, with further unfolding exposing stigmas of more basal flowers.
3. Female-biased and female inflorescences were much narrower, unfolded from smaller buds, and the first stigmas exposed were already receptive (receptivity was determined by pollen germination tests in vivo, that are not presented here). The increase in the number of receptive stigmas was more gradual than in balanced hermaphrodite inflorescences, beginning with about 5 stigmas (versus 20-30 stigmas) and ending at inflorescence length of 3-4cm (versus 2-3cm in balanced hermaphrodites).

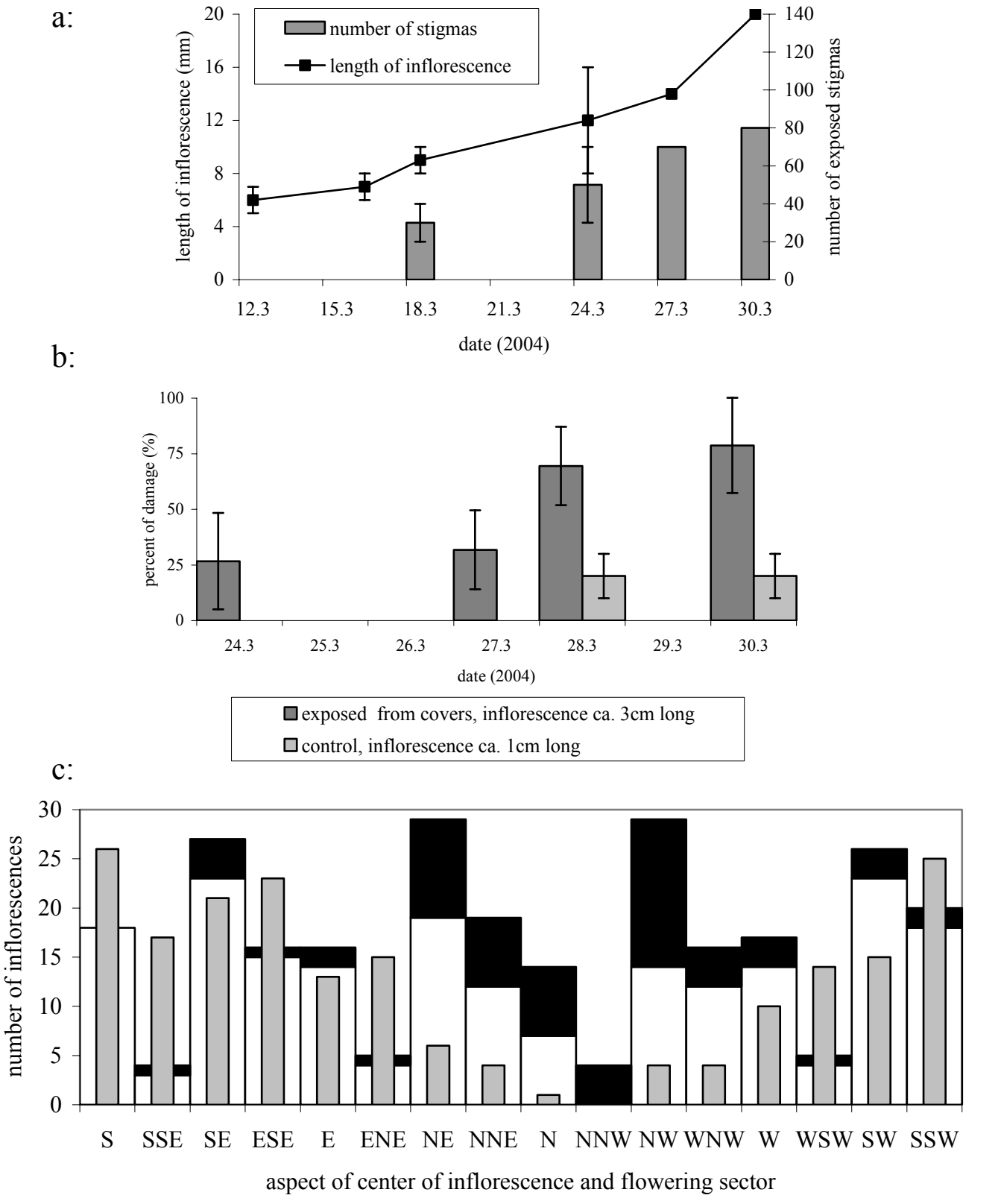


Figure 14: Inflorescence phenology of *Fraxinus excelsior*. **a**: Lengthening of an hermaphrodite inflorescence and gradual exposure of stigmas. **b**: Dependence of frost damage on inflorescence length in a hermaphrodite inflorescence. **c**: Anthesis in male inflorescences ("anther spheres") from south to north.

Frost damage (plate 4) was larger in lengthened male inflorescences than in not lengthened ones ("anther spheres"), as observed in comparing different trees on 6-8.4.2002 (30% versus 0 damage, respectively). Male trees withstood the cold week 2-10.4.2003 in the waiting phase almost without damage (five of 39 trees suffered light damage), whereas in this week opened hermaphrodite and female inflorescences were totally destroyed. The apparently dead inflorescences did sprout further flowers later, but the fruit-set of damaged trees was reduced down to 10% of a normal crop. In total, eight of 13 female and hermaphrodite trees were severely damaged and three suffered light damage. Inflorescences unfolded much quicker when covered. Using this effect, the susceptibility to frost of hermaphrodite inflorescences in a natural unfolding stage (1cm long) and in a "later" unfolding stage (accelerated phenology, 3cm long) on the same branch was compared. The former suffered some damage, but the latter were mostly destroyed by frost (figure 14b, plate 4).

Pollination and fruit

Most pistils in the samples had germinating pollen grains on their stigmas, the category 11 to 30 grains held the largest number of pistils. The median number of germinating pollen grains for all pistils was seven, 24% of the probes had more than 20 germinating pollen grains. 4-22 grains were the range 1^{st}-3^{rd} quartiles for the non zero stigmas. Pollen tubes were found in smaller numbers, usually up to three were found in the stigma and less in the style and ovary (figure 15). Mostly one pollen tube reached the ovules (median of pollen tubes in pistils with pollen tubes is 1 and 1^{st}-3^{rd} quartile are 1 and 2). In the few cases where two pollen tubes reached the ovules they were conspicuously parallel entering the embryo sac.

The number of pollen grains and pollen tubes correlated significantly between the different stages along the pistil (table 8). The slopes of the regressions, taken as an assessment of the intensity of pollen tube competition, were ca. 20-30:1 from germinating pollen grains to pollen tubes in the stigma and 5:1 from pollen tubes in the stigma to pollen tubes in style.

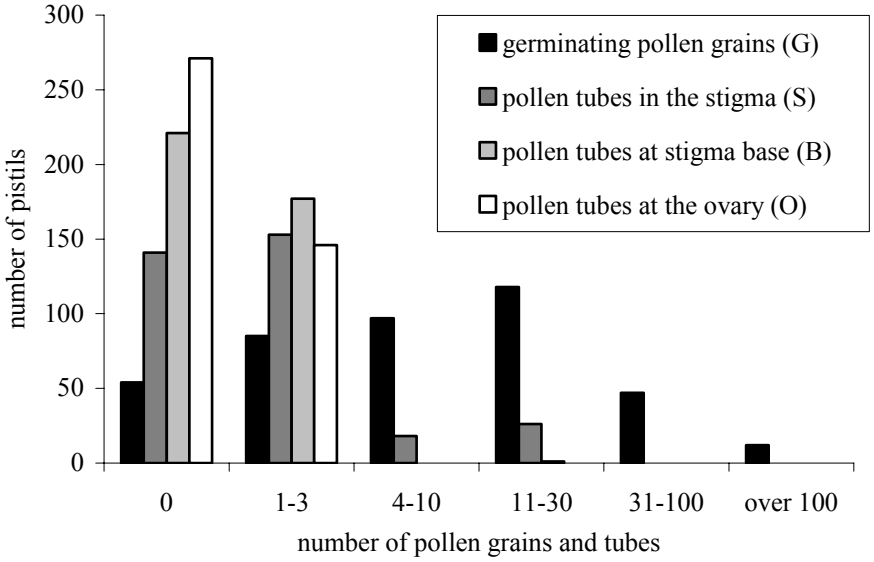


Figure 15: Pollen grains and pollen tubes in the analysed probes

Table 8: Pearson product moment coefficients and regressions between the number of pollen grains and pollen tubes at different stages along the pistil for all probes and for successfully pollinated probes only. P<0.0001 for all coefficients, except where noted. Abbreviations: G=Germinating pollen grains, S=Pollen tubes in the stigma, B=Pollen tubes at stigma base, O=Pollen tubes at the ovary.

stages	all pistils	pistils with pollen tubes at the ovary
G to S	0.37; S = 2.0 + 0.048·G	0.29; S = 3.8+0.031·G
S to B	0.57; B = 0.29+0.19·S	0.55; B = 0.85+0.18·S
G to B	0.14 (p=0.05); B = 0.74 + 0.0059·G	no correlation (p=0.7)
all to O	G to O: 0.30; S to O: 0.40; B to O: 0.47	almost all O=1

Thrips (*Taeniothrips inconsequens* Uzel) and the nitidulid beetles *Epuraea melanocephala* Marsham were occasionally found in inflorescences. Birds (blue tits – *Parus caeruleus*) were observed picking in inflorescences of all tree genders. The median visit time per twig was between 2 and 6 seconds on different dates, and picking times were bimodal distributed – most visits were short, some visits took up to 25 seconds for a single twig. One bird was caught in 2005 on a female tree with 75 pollen grains of *F. excelsior* on ca. 1cm^2 on its head.

Self-compatibility varied among the individual trees. In eight trees checked, five had significantly more young fruit on exposed than on covered twigs (Mann-Whitney rank sum test p<0.001 in four, p=0.019 in the fifth tree), whereas in the other three trees fruit set was not significantly different (in one tree more fruit on exposed twigs, but not significantly

p=0.23, in other two trees the same number of fruit). The five trees were two female-biased hermaphrodites, two balanced hermaphrodites and one male-biased hermaphrodite, the three trees were one of each gender. In *Fraxinus pennsylvanica* exposed and covered twigs yielded the same fruit number and thrips were found inside two of the covers.

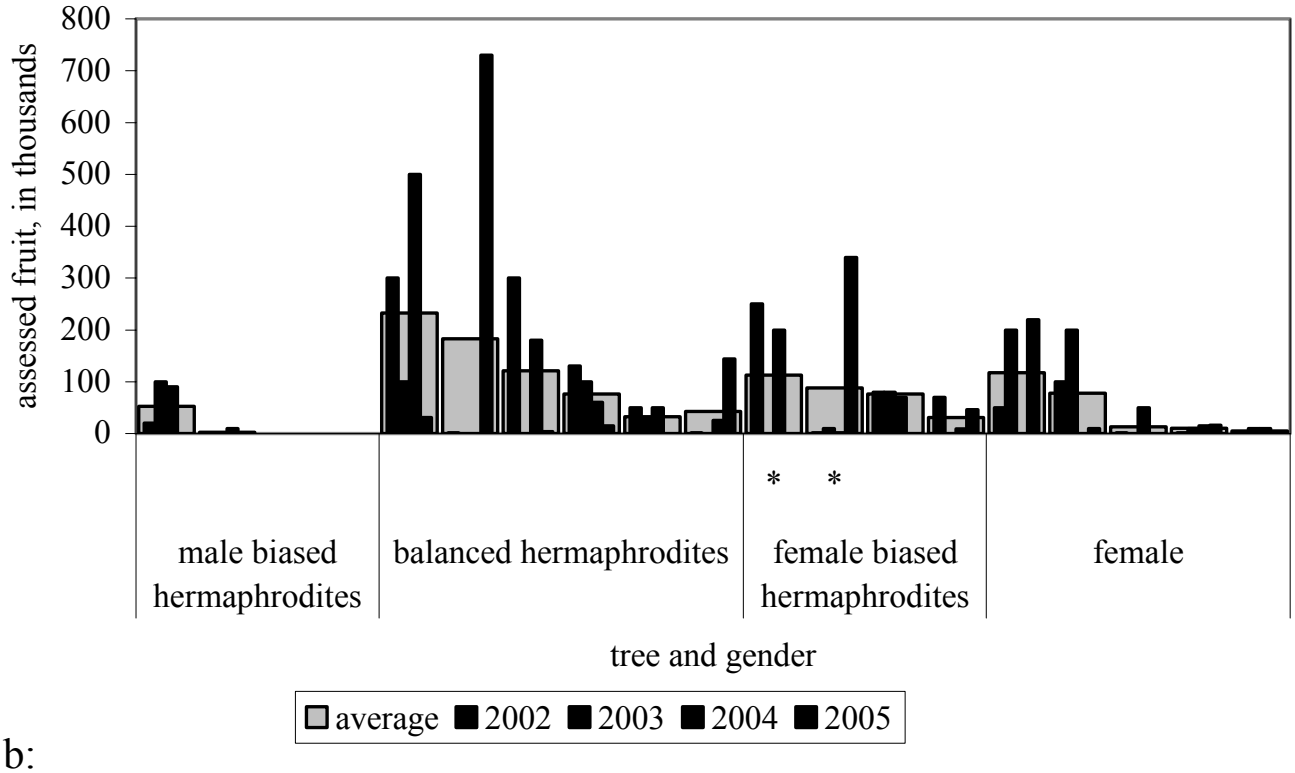
Empty fruit frequency was below 10% in most trees (in 2004, it was above 15% in only two trees), 1-7% of the fruit per tree had two seeds and three seeded fruit were found but rare. No significant correlation was found to tree gender and data were too few to check the correlation of the seed per fruit rate for the same trees in different years. The 100-fruit weight was between 7.2gr and 10.6gr (median 9.5gr, 13 trees, air dried weight). One tree had especially heavy fruit – 17.9gr per 100 fruit, this tree was also exceptional in its flower morphology (plate 2) and gender distribution (Tal 2003). Table 9 presents the number of fruit per infructescence and twig, and the percent of empty fruit for studied trees in 2004 and 2005. Most studied trees were different between the years.

Table 9: Fruit per infructescence and twig, and percent of empty fruit.

	fruit per infructescence	fruit per twig	empty fruit
2004 (13 trees)	9-82 (median 46)	31-517 (median 254)	1-39% (median 8%)
2005 (14 trees)	13-47 (median 23)	54-311 (median 144)	0-16% (median 2%)

The total yield of *F. excelsior* in the stand was 1-1.5 million fruit per hectare per year. Balanced hermaphrodites, followed by female-biased hermaphrodites were the most prolific fruit producing trees in the stand in the four study years. Female trees produced a lesser crop and male-biased hermaphrodites produced a very small part of the total (figure 16a). Most trees strongly fluctuated in their fruit production between years, but the fluctuations were not synchronised among trees, so that overall yearly crop in the stand was quite constant (figure 6). The only effect on it was the cold week during flowering in 2003, which damaged large parts of most trees' female flowers (figures 5 and 12, and results after figure 14). The total number of fruit per tree in the study years did not correlate with the average flowering intensity for all trees (Spearman rank order coefficient p=0.18 for all 19 trees), but taking out the tree with the maximal crop and the tree with the lowest flowering intensity, flowering intensity correlated negatively and significantly with the total crop per tree (Spearman rank order coefficient -0.65, p=0.005). On three occasions, trees produced fruit mainly on one half of the crown, although they flowered in the whole crown.

a:



b:

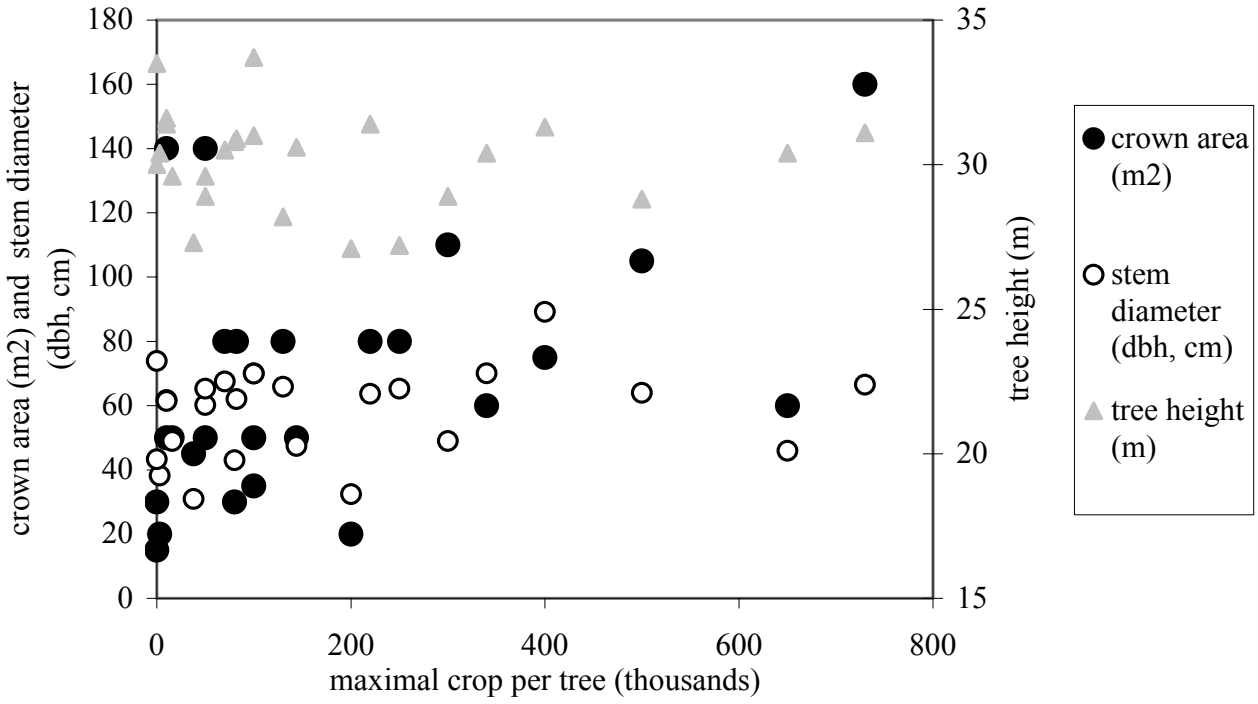


Figure 16: Fruit in *F. excelsior* in the study years. **a**: Fruit per tree after gender type (black) sorted after the average over the four years (grey). * - these two trees were classified as balanced hermaphrodites in the years of large crop 2004 and 2005 (respectively). Total fruit of five other female-biased hermaphrodite trees in 2005 were 650,000, 400,000, 100,000, 41,000 and 38,000 and of another female tree 3000. **b**: Maximal crop per tree in the study years in respect to tree size (crown area, stem diameter and tree height). For three occasions, in which fruit was produced only in a half of the crown, the double crop is presented.

The studied trees with most fruit in 2004 had 47kg, 21kg and 16kg in total (air dried weight). Three trees produced 8-9kg, three 5kg and four 1-3kg. The maximal crop per tree was significantly correlated with its crown area but neither with its stem diameter nor with tree height (figure 16b, Pearson product moment coefficients 0.44, 0.19, -0.08 with $p=0.027$, $p=0.36$, $p=0.71$, respectively). The regression slope was 2325 (maximal) fruit per square meter crown area.

Acer platanoides

Gender sequences of the four large trees studied in 2004 were male-female-male (protandrous, duodichogamous) in one tree and female-male (protogynous, with very few female flowers following) in the other three large trees. Three of four small trees were protogynous and one protandrous. The gender sequences of the four large trees were the same in 2005, the four small trees did not flower, and additional two small trees were one protandrous (duodichogamous) and the other protogynous. The overall relation of protandrous to protogynous trees was thus 3:7.

Flowering intensity was high in 2004 in all trees. The number of inflorescences of the small trees was very low in respect to the large trees (see fruit assessment below). The flowering period consisted of the sunny periods 10-12.4, 14-18.4 (ending with a rainy 19.4) and 20-22.4, corresponding approximately to the changes in gender phases (figure 18 and figure 43 in the appendix). In 2005 the large trees flowered scantly, the four small trees did not flower and two additional trees flowered scantly.

Flowering and unfolding of the inflorescence up to a length of 6cm went hand in hand. As the inflorescence lengthened, the number of opened flowers accumulated (figures 17 and 19). Further lengthening was too gradual to be reliably documented.

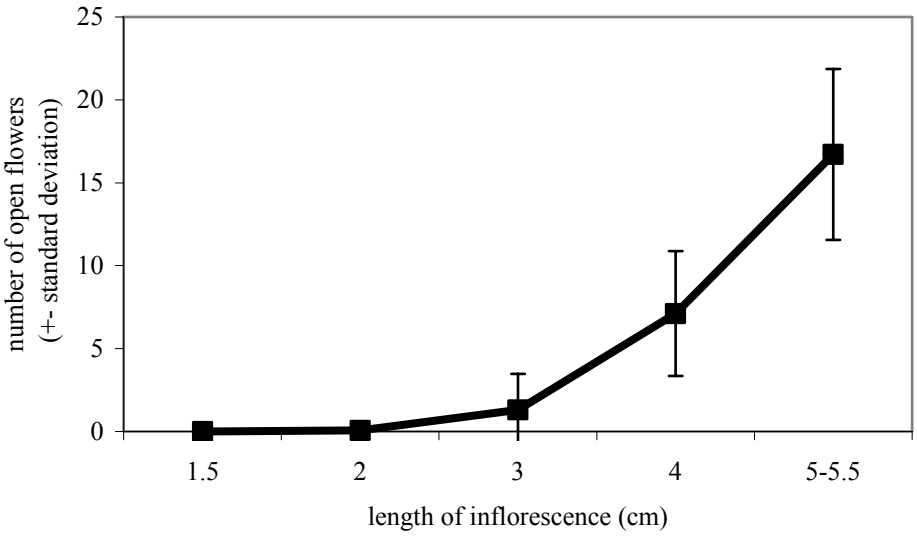


Figure 17: Inflorescence unfolding and number of flowers in anthesis, averaged over 120 inflorescences of one tree, 2004.

The flowering in the large trees proceeded from lower crown to upper crown (figure 18, the presented results are for the large protandrous tree) and from within outwards along the branches (figure 19). The inflorescences were mostly synchronised in their gender phases, except for some overlap between lower and upper crown. The first male phase had more flowers in the lower crown than in the upper crown, whereas the second male phase had more flowers in upper crown (16m vs. 30m on 12.4 and 27.4, for both t test for the number of flowers $p<0.001$). The maximal number of female flowers per inflorescence was the same in the three heights (16m on 16.4 versus 30m and 24m on 20.4, t test $p=0.4$).

Vertical differences were statistically significant on almost all comparisons on all dates - Kruskal-Wallis one way analysis of variance (ANOVA) on ranks $p<0.001$ on all dates together, Mann-Whitney rank sum test $p<0.001$ between all pairs except 16m and 24m on 16.4 ($p=0.01$), and not significant between 24m and 30m on 20.4 and 23.4 ($p=0.7$ and 0.2 respectively).

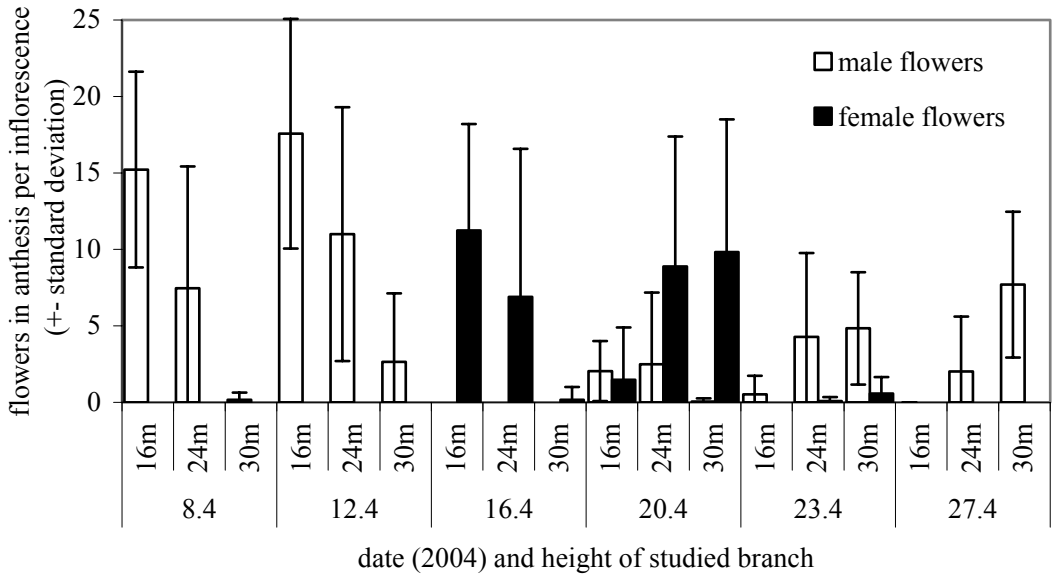


Figure 18: Overview of flowering phenology in three branches at different heights on a large tree.

The anthesis in the branches was analysed also along the horizontal gradient from the basis of a branch system to its periphery (0cm to 100cm respectively, figure 19). All graphs show instances of a horizontal gradient from within the crown outwards (from 0-20cm towards 80-100cm). The following differences were statistically significant (ANOVA on ranks $p<0.001$, except 30m on 12.4 $p=0.04$, and 24m on 23.4 $p=0.01$):

1. First male phase: At 24m on 8.4 and at 24m and 30m on 12.4. In both the gradient in inflorescence length is likewise conspicuous.
2. Female phase: At 24m on 16.4 and on 20.4.
3. Change to second male phase: At 24m on 20.4.
4. End of second male phase: At 24m on 23.4 – apparently an opposite gradient but actually representing the end of flowering that still lasts only on the outer end of the branches.

Most of the other combinations of height and date represent branches before or at the end of a flowering phase (e.g. 30m and 16m on 8.4 respectively, 16m on 12.4 and 16.4).

The three protogynous large trees had a reciprocal gender sequence to the protandrous tree, and were on 6-12.4 female and 16-23.4 male (after that came another female phase with a very low intensity (few flowers). They presented similar vertical and horizontal patterns. Two of three small trees near the large protandrous tree of figure 18 were protogynous and flowered with the same timing of gender changes (i.e. presented the reciprocal gender) but due to their size, their flowering was quantitatively in a very limited scope.

At flower level the following phenomena were noted (plate 6):

1. Male and female flowers differed in disc color – the former yellow the latter green.
2. Stamens bent inwards at anthesis (commonly one after the other) and the anther opened inwards.
3. The first flowers in an opening bud leaned southwards.

Flowering period in 2005 was between 7.4 and 29.4 and of low intensity. The flowers of all trees were quickly devoured by aphids and nitidulid beetles, and the full sequences and phenology could not be followed. Flowering in 2006 was full and began about a week later (the end of winter was exceptionally late).

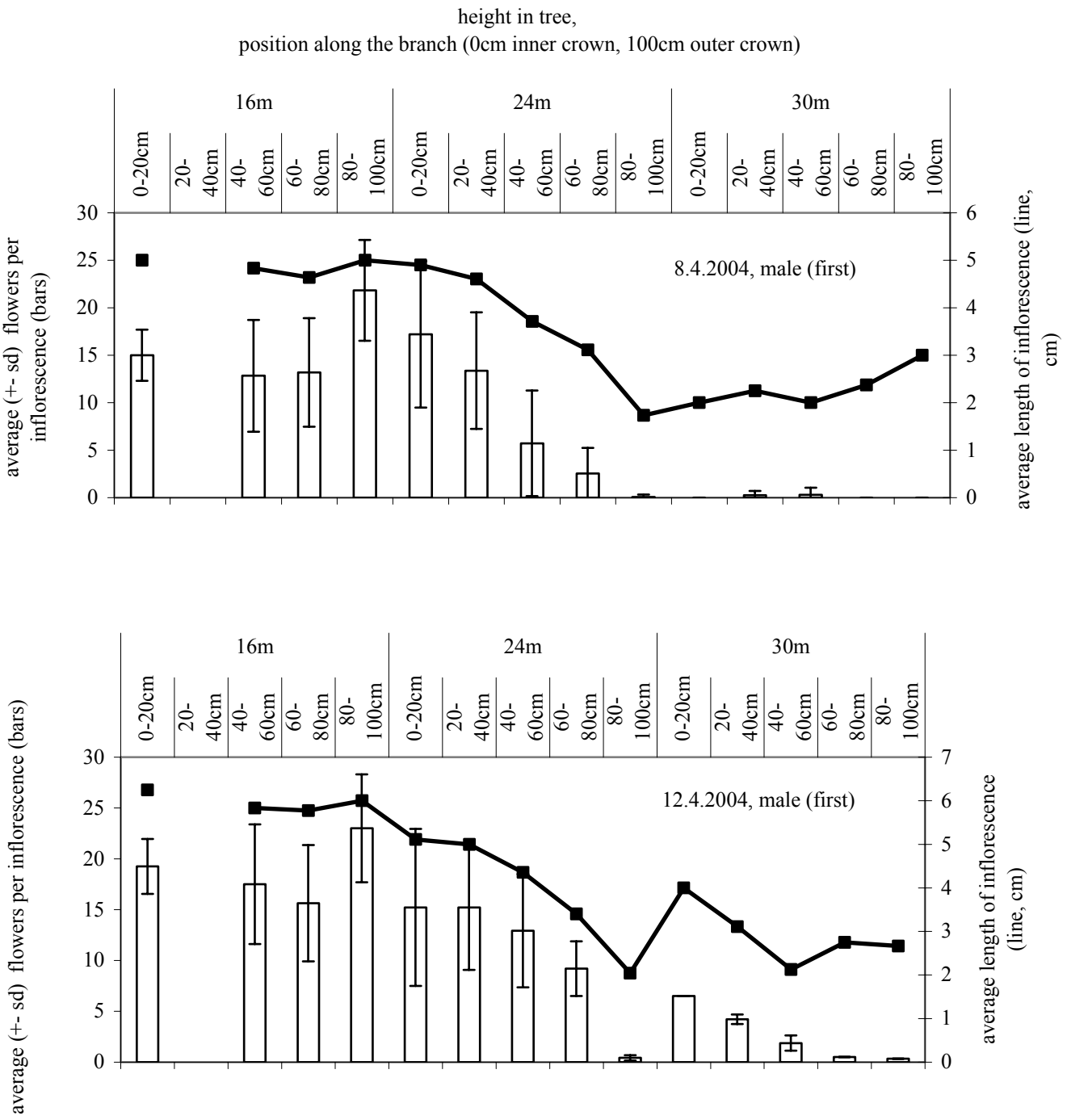
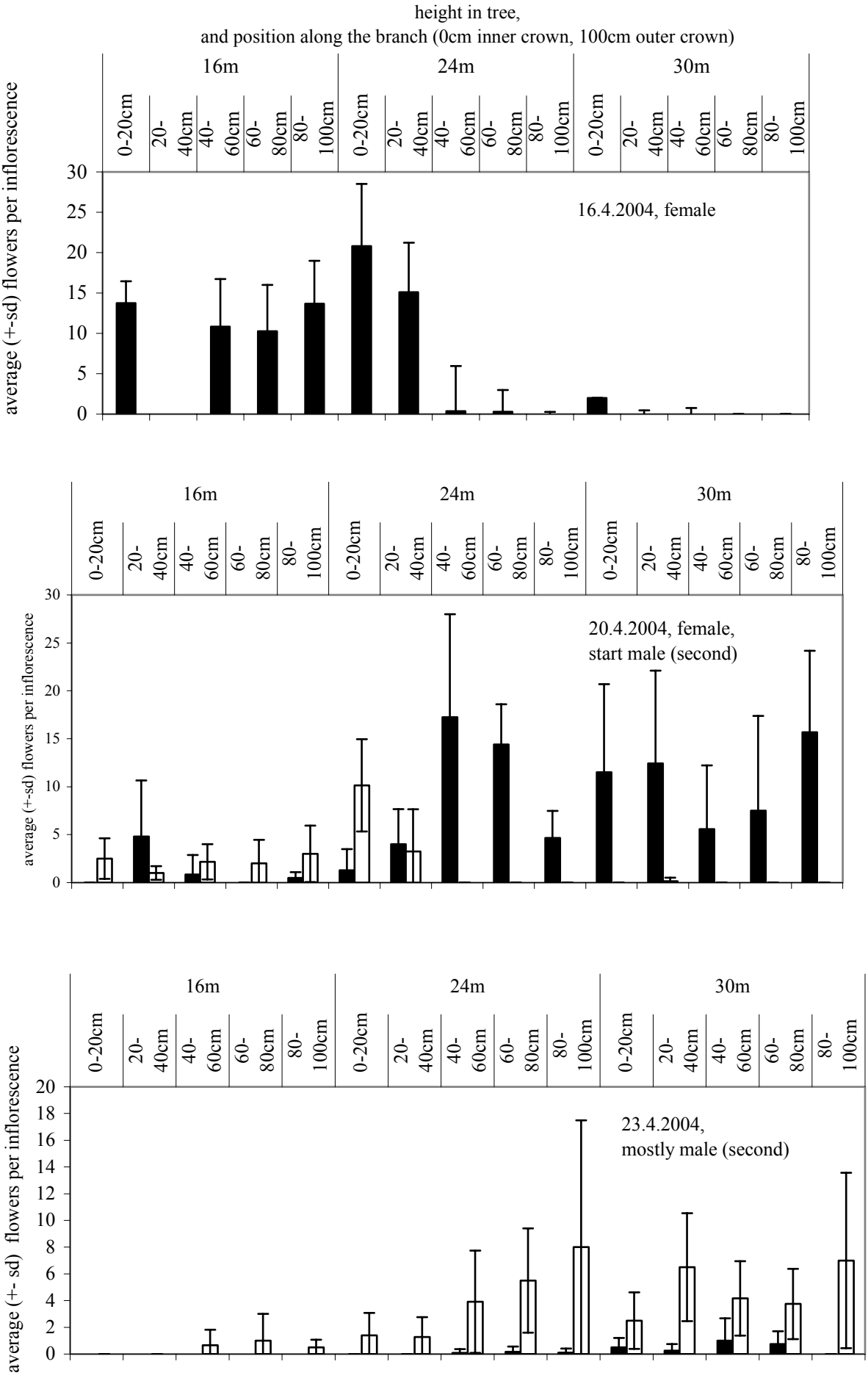


Figure 19: Details of flowering phenology in three branches at different heights on the large protandrous tree of figure 18. Flowers at anthesis per inflorescence are presented for five consecutive checks as the tree went through a male-female-male gender sequence, within each branch after the radial distance from branch basis. The first two graphs present the first male phase **(white)** and include the average length of the inflorescences. The following three graphs (next page) present the beginning and end of the female phase (**black**, with the beginning of the second male phase in **white**), and the second male phase (with rests of the female phase, the graph for 27.4 was left out).


height in tree,
and position along the branch (0cm inner crown, 100cm outer crown)
16m
24m
30m
0-20cm
20-40cm
40-60cm
60-80cm
80-100cm
average (+-sd) flowers per inflorescence
16.4.2004, female
20.4.2004, female,
start male (second)
23.4.2004,
mostly male (second)

Taeniothrips inconsequens (Thrips) and black *Epuraea melanocephala* (nitidulid beetle) were abundant in the inflorescences. They performed typical movements at disturbance – the thrips retreated from flowers to inflorescence basis and the beetles fell out of the flower a few seconds after shaking them. Stamens reaching anthesis usually bent to the center of the flower, and clearly touched the emerging beetles. Blue tits (*Parus caeruleus*) predated in the inflorescences (median visit time two seconds, single visits up to 13 seconds). *Bombus* spp. (mostly *B.* cf. *terrestris*) visited flowers for three second in median (range 1-4 seconds), contrasting with *Andrena* cf. *haemorrhoa* visiting in median eight seconds per flower (single visits up to 24 seconds, Mann-Whitney rank sum test between *Bombus* and *Andrena* $p<0.001$, plate 8).

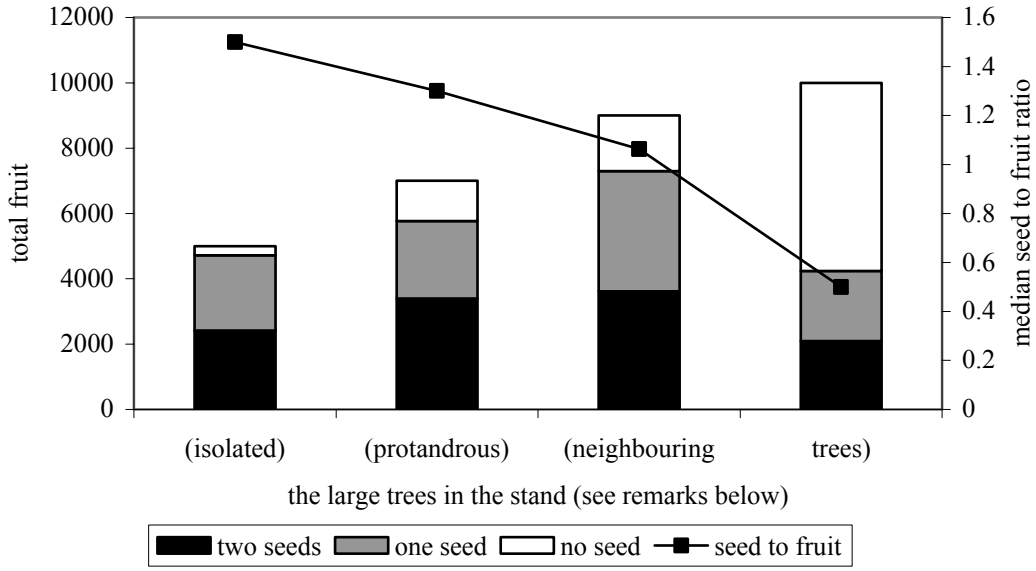


Figure 20: Fruit production in the stand. Crops of the four large trees are subdivided after the number of seeds per fruit (practically all fruit with two mericarps). Trees are sorted after the median seeds to fruit ratio over all inflorescences. The remarks at the x-axis denote the protandrous tree (the others were protogynous), the relatively isolated tree (40m to next con-specific) and the two adjacent trees (with the same gender sequence).

Fruit sets of the four large *Acer platanoides* trees in 2004 were between 5,000 and 10,000. The total crop in the stand, ca. 30,000 fruit, was produced to 80% by three trees, and the four large trees produced 99% of the fruit in the stand. The small trees produced 50 to 100 fruit each. No fruit was produced in 2005. The total number of fruit per tree was positively correlated with tree size (figure 20, Pearson product moment coefficient for tree height 0.94, $p=0.06$, stem diameter 0.92, $p=0.08$ but not for crown area $p=0.3$) and negatively correlated

with the seed to fruit ratio (figure 20, Pearson product moment coefficient –0.92, p=0.08). The seed to fruit ratio was between 30% and 70%. The highest seed to fruit ratio was in a relative isolated tree, however the two large neighbouring trees with the relative low seed to fruit ratio had the same gender sequence and were synchronised. No patterns were found in respect to gender sequences or position in the crown. The proportion of fruit with three mericarps was between 0 and 1.3% per tree. Fruit set in four undamaged covered inflorescences did not significantly differ from 11 exposed inflorescences (Mann-Whitney rank sum test p=0.8). Fruit number per infructescence was significantly higher in upper crown than in lower crown and differed significantly among the three marked branches of figure 18. The branches at 16m, 24m and 30m had in average (±standard deviation) 8.1±2.4, 10.2±4.5 and 16.9±10 fruits per infructescence respectively (medians 8,10 and 14.5 respectively, Mann-Whitney rank sum tests: 16m-30m p=0.006, 24-30m p=0.014, 16m-24m p=0.024).

Acer pseudoplatanus

Gender

Three quarters of the trees in the stand were protandrous, one quarter were protogynous, leaving one tree expressing only male gender (figure 21). The difference from a 1:1 distribution is significant (χ^2=17 (with Yates' correction for one degree of freedom), p<0.01). No tree was found to change its gender sequence between 2004 and 2005.

The third phase in both sequences was usually male and appeared in most trees (figures 21, 22 and 24), at least in the largest inflorescences. In two trees per year few female flowers appeared as a forth phase, and on the male tree in 2005 few female flowers were found in the third phase in a few inflorescences. Most embryonic flowers in the buds of the male tree shortly before bud opening had pistils similar to those of male and hermaphroditic flowers on other trees (plate 2).

Most flowers in the inflorescence were male, and the phase with the largest number of flowers was the first male phase in both tree types. Comparing the number of flowers at corresponding stages in protogynous and protandrous trees in 2005 yielded the following results (figure 22):

1. Protogynous trees had fewer flowers in the female phase (median category 6-10 vs. 21-30, Mann-Whitney rank sum test p<0.001).
2. Both types had a similar number of male flowers in the first male phase (median category 41-60, p=0.6).
3. Protogynous trees had somewhat less male flowers in the second male phase (median category 6-10 vs. 11-20, p=0.02 for 8 protogynous and 27 protandrous trees having this phase).

The functional femaleness of trees, calculated with the formula F / (F+M·E) (Lloyd 1980), with F and M for each tree as the middle of the range of these flower numbers and E as the sum of F to the sum of M over all trees (E=0.38, 2005), changed very gradually with tree rank (figure 23a) and reached 0.8 at maximum. Protogynous trees scored as relatively male, whereas protandrous trees covered the whole range, some of them were quite female but the most were above 0.5 femaleness.

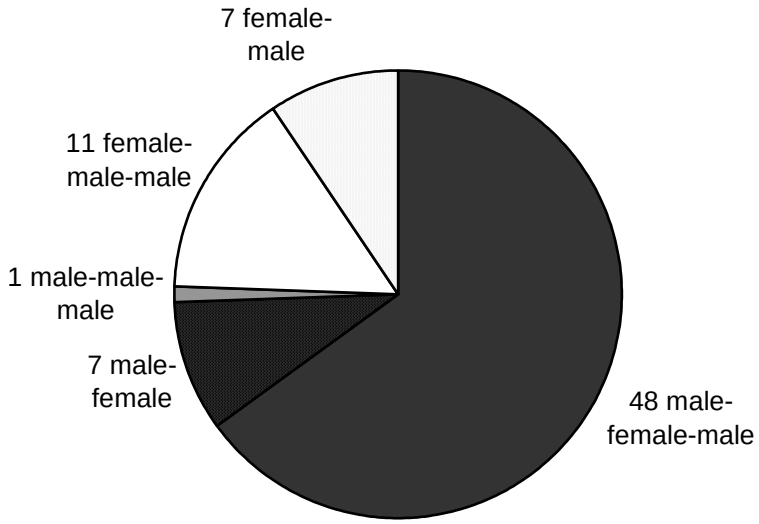


Figure 21: Distribution of gender sequences in the stand (data combined from 2004 and 2005)

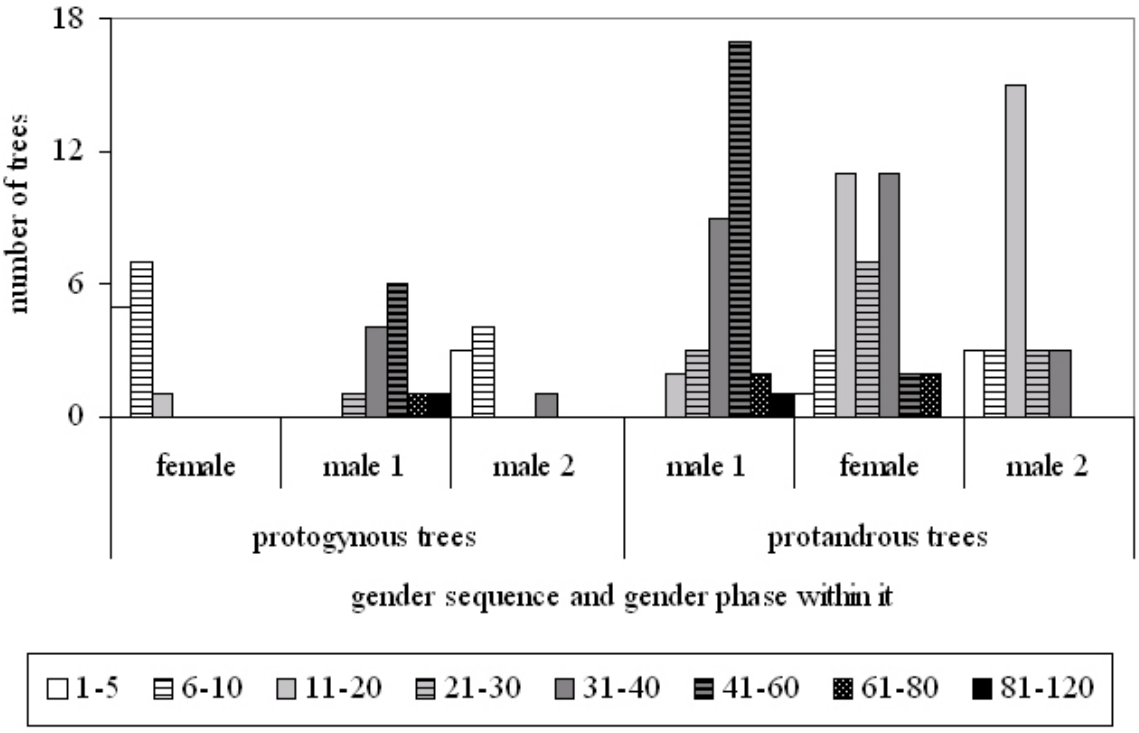
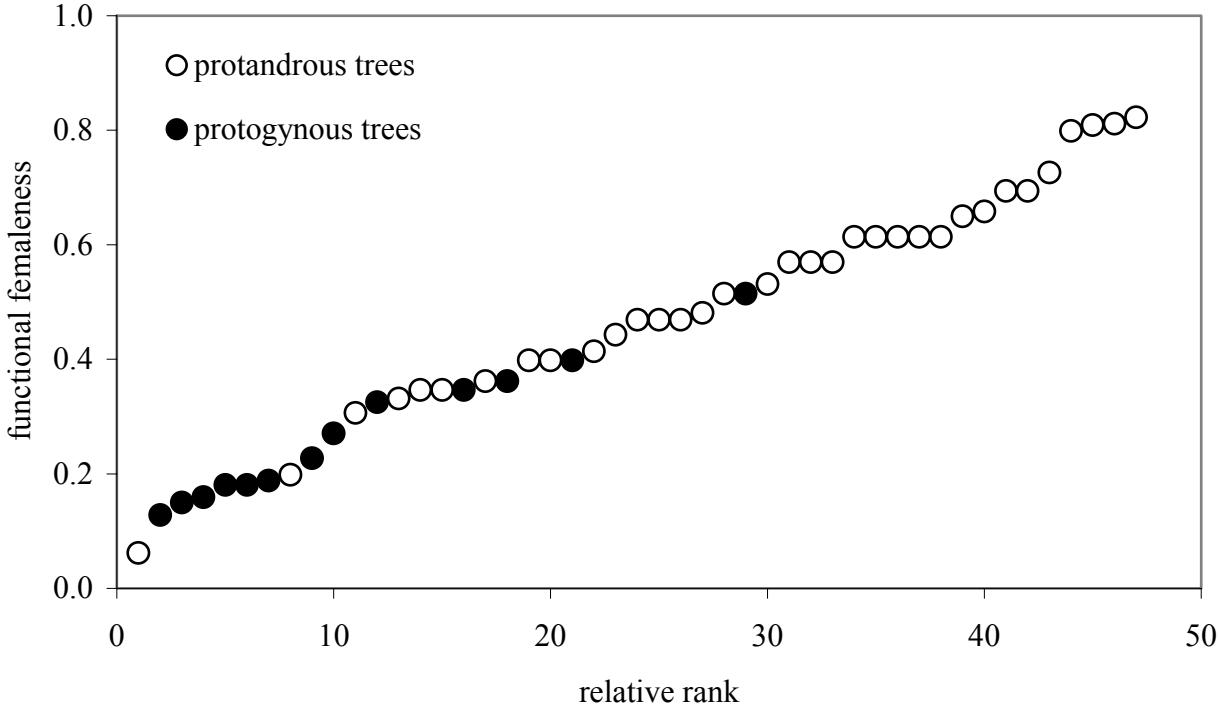


Figure 22: Number of flowers after phases in 13 protogynous and 37 protandrous trees in large inflorescences (2005), in categories. The second male phases was missing in 15 trees.

a:



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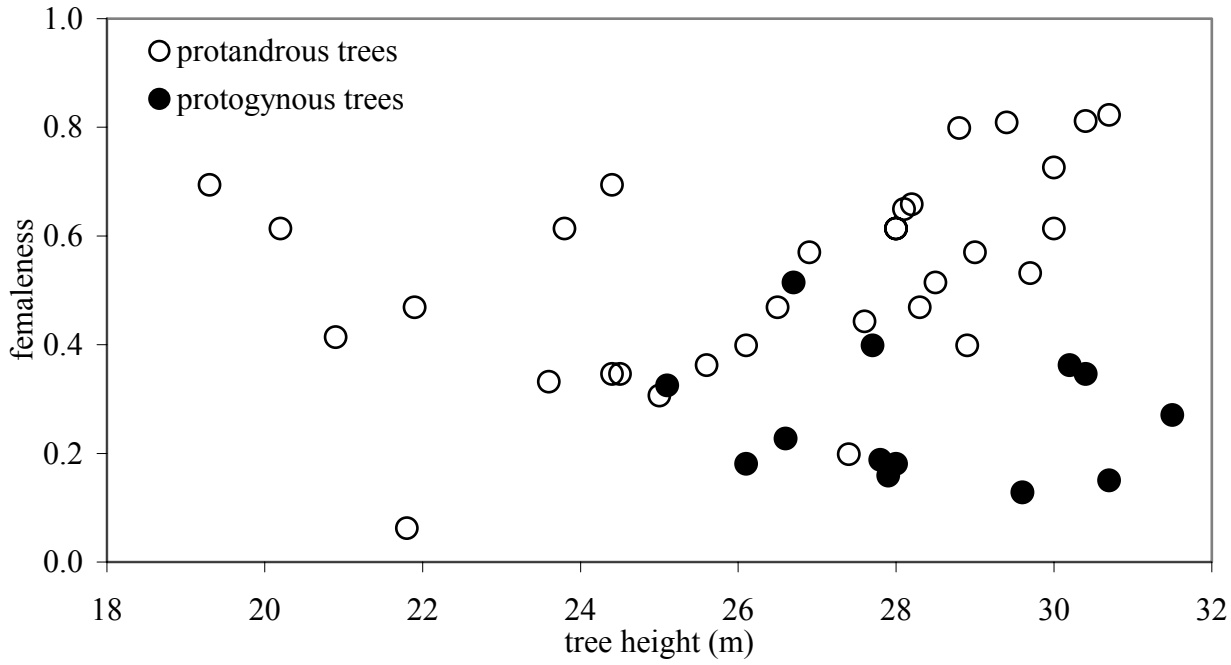


Figure 23: Functional femaleness in 47 trees in the stand (**a**) and its correlation with tree height (**b**). Trees are denoted after their gender sequence. Note that the upper graph is the projection of the lower graph on the y axis.

Protandrous trees were significantly smaller than protogynous trees, both in stem diameter (t-test, $p = 0.026$) and in tree height (Mann-Whitney rank sum test, $p=0.029$). The difference is however mainly due to the lack of small protogynous trees. The types did not differ significantly in these parameters ($p>0.8$) when only trees over 25m height and 30cm stem diameter were compared. In protandrous trees higher than 25m, femaleness and heights were strongly and significantly correlated (figure 23b, Pearson product moment coefficient 0.72, $p=0.0002$) whereas in protogynous trees no significant correlation was found (Pearson product moment coefficient –0.16, $p=0.6$). In neither of the groups was such a tendency found in respect to crown area and stem diameter.

Pollen diameter was distributed around 32.5µ and 77% of all grains were within 30-35µ. Protogynous and protandrous trees did not significantly differ from each other as groups, but within each of them trees could be separated into significantly differing subgroups: Two groups of five among ten protogynous trees (ranging 34µ-30µ in median, ANOVA on ranks for all $p<0.001$, Mann-Whitney rank sum test between the two groups $p<0.001$) and three groups among 28 protandrous trees (ranging 35µ-27µ, mutually differing subgroups, overall ANOVA on ranks $p<0.001$, plus an exceptional tree with median pollen grain diameter 24µ). However, also within-tree variance was found. In eight of 13 comparisons of different probes from crown top differences in pollen diameter were significant (Mann-Whitney rank sum test $p<0.01$, in six $p<0.001$).

Individual trees also differed in style length, stigma thickness, length of papilla and maximal lobe length. Whereas in some trees the stigma lobes grew up to 7mm each and curled one and even two rounds, in others they reached 1mm at their maximal spread (plate 5). The difference in maximal lobe length was not related to the grade of pollination and was not quantified in respect to gender sequence, but trees with conspicuously short stigmas were protandrous whereas thick and long stigmas were more frequent in protogynous trees.

Flowering phenology

Whereas in 2004 practically all trees flowered in full intensity, in 2005 only about a half flowered in full intensity and the others mostly in partial or scant intensity (figure 5). In 2005 trees with a larger stem diameter and a larger crown area flowered in a higher intensity than smaller trees (Pearson product moment coefficients for stem diameter 0.26, $p=0.03$; crown

area 0.22, p=0.06; and tree height 0.2, p=0.1, not significant). Flowering intensity did not significantly correlate with the gender sequence (Mann-Whitney rank sum test p=0.53) nor with the time of flushing.

Flowering intensity was further decimated by much herbivore damage to the inflorescences, which destroyed a large proportion of the flowers. Herbivore damage was caused mainly by different homopteran larvae and adult aphids and appeared most often as black anthers and stigmas or inflorescence parts smeared with sticky honeydew. Of 59 trees flowering in 2005, the male phase was damaged in 39 (66% of flowering trees, fully damaged on 20 trees, partially damaged on 19 trees) and the female phase was damaged in 11 trees (19% of flowering trees, partial damage).

The flowering took place in both years in the same period, and in both years, the main flowering in the first phase was at a warm and sunny period, and ended in most trees in a rain period (3-6.5.2004, 7.5.2005 – figure 43 in appendix). The beginning and end of the second flowering phase were temporally smeared and did not relate to weather fluctuations (figure 43 in appendix). Also, the overall and main duration of the female phase in 2005 were significantly and negatively correlated with the dates of their beginning, with the regressions (all p's<0.001):

$$\text{Overalll duration of female phase} = 11.1 \text{ days} - 0.45 \cdot \text{days after 6.5}$$

$$\text{Duration of main female flowering} = 5.8 \text{ days} - 0.22 \cdot \text{days after 6.5}$$

The slopes are such that a female phase starting ten days later is 5 days shorter in total, and its main flowering is two days shorter. Starting and end dates of flowering correlated significantly in both years (table 10).

Table 10: Starting and ending dates of flowering – correlation and regression. The dates are calculated from the reference date.

year (reference date)	Pearson product moment coefficient	regression, E=end and S=start of flowering
2004 (23.4)	0.38, p=0.04	E = 27.3 (days) + 0.54 · S
2005 (25.4)	0.28, p=0.05	E = 27.0 (days) + 0.25 · S
only protogynous	0.60, p=0.03 (protandrous p=0.12)	E = 23.6 (days) + 0.42 · S

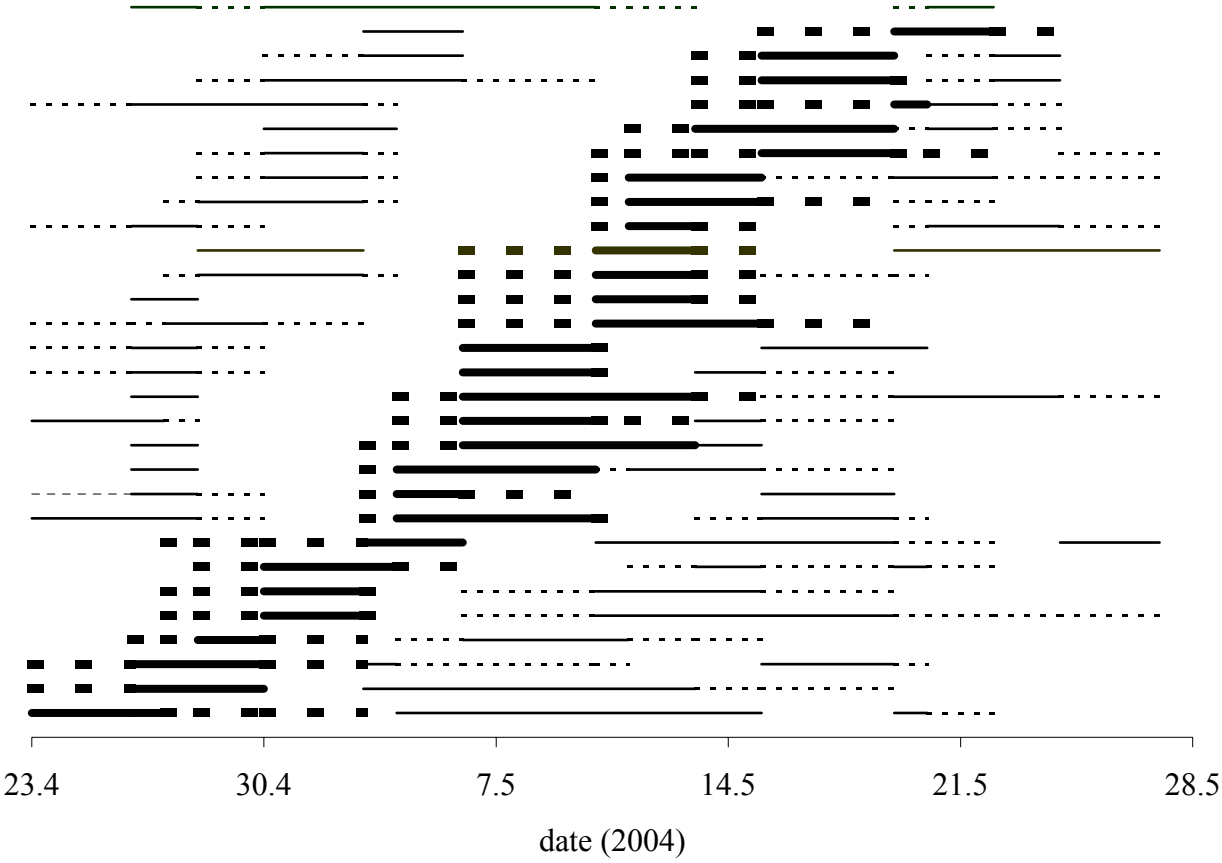
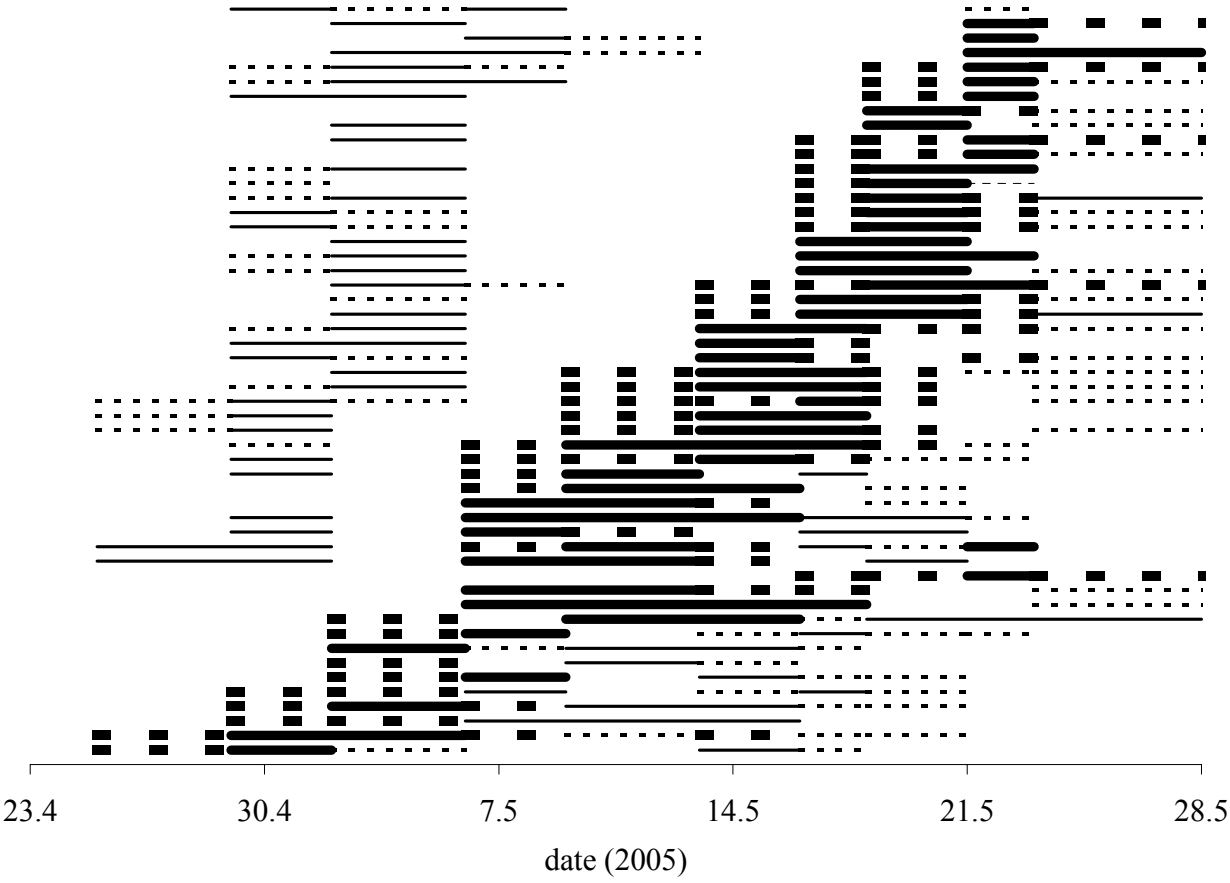


Figure 24: Phenology diagrams for *A. pseudoplatanus* in 2004 (up) and 2005 (down). Line types: Thick – female flowering, thin – male flowering, continuous – main period of flowering, broken – residual (initial or final) periods of flowering. Note in both years the multiple male phases in protogynous trees, the upper male tree, and in 2005 the late flowering protogynous trees and the second female phase in two trees.



Each flowering phase took about a week (figure 24, table 11), protogynous trees had a longer male phase than protandrous trees, and their male flowering in 2004 was longer than in 2005. The duration of female flowering did not differ between protandrous and protogynous trees nor between years (Mann-Whitney rank sum test p's above 0.3). Of all comparisons for the male flowering, the following differed significantly (Mann-Whitney rank sum tests):

1. The duration of male flowering between 2004 and 2005, in protogynous trees (overall $p<0.001$, main $p=0.03$) and in protandrous trees (overall $p=0.003$, main $p=0.09$, not significant).
2. The first male phase in 2004 between protandrous and protogynous trees (overall $p=0.001$, main $p=0.07$, not significant).
3. The first pause in protandrous trees differed significantly from the second pause (Mann-Whitney rank sum test, both years $p<0.001$), and also from the first pause in protogynous trees (Mann-Whitney rank sum test, $p=0.001$ in 2004, $p<0.001$ in 2005).

Table 11: Median durations of female and male flowering and of the pauses between them in protandrous and protogynous trees. Overall flowering refers to both brocken and continuous lines in figure 24 and main flowering refers to the continuous lines only. For male flowering the median durations of the two male phases are presented in parentheses.

study year	gender sequence	female flowering		male flowering		pauses	
		overall	main	overall	main	first	second
2004	protandrous	8	4	11 (6+5)	6 (3+2)	6	0
	protogynous	7.5	3.5	13.5 (11.5+1.5)	7 (7+0.5)	2	0
2005	protandrous	7	4	8.5 (7+3)	4 (4+0)	7	0
	protogynous	7	3	9 (7+0)	3 (3+0)	0	0

The synchronicity indices of the whole flowering periods for *A. pseudoplatanus* trees were 0.82 and 0.86, the steps 1.8% and 1% and the duration to deviation (p/SD) 9.8 and 6.3 for 2004 and 2005 respectively. The analysis of synchrony of the single gender phases and the relations among them (table 12) showed that:

1. The highest synchronicity indices and the lowest steps were of phases of reciprocal gender (0.5-0.6, 2.4%-4.5%), then of each stage by itself (0.3-0.5, 3.5%-24%, mostly above 8%), and then of other pairs of stages (0.3-0.4).

2. Protandrous flowering was more synchronised than protogynous flowering in both gender phases, as best seen on the steps, being two to five folds larger in the latter than in the former.
3. Gender phases of protandrous trees in 2005 were more synchronized within themselves than in 2004 (steps about half as large). Protogynous female flowering was as synchronised, protogynous male flowering less synchronised in 2005 than in 2004.
4. The step, independant of tree number, was the most appropriate index to compare the gender sequence groups as they differed in tree number.

Table 12: Synchronicity indices, steps and average duration to standard deviation of starting dates (p/SD) for gender phases in the flowering of *A. pseudoplatanus* in 2004 and 2005. Shaded - female phases, thickly bordered - male phases, * - in intermediate cells indices including the two adjacent phases (diagonal indices refer to the female phases). Indices involving the male phase of protogynous trees are averages of the indices with and without the second male phase.

Synchronicity	2004					2005				
gender phase	1st	*	2nd	*	3rd	1st	*	2nd	*	3rd
protandrous	0.49	0.28	0.46	0.35	0.4	0.63	0.31	0.52	0.4	0.42
*	0.57	0.31*	0.58			0.66	0.38*	0.49		
protogynous	0.49	0.32	0.51			0.39	0.32	0.32		
Step	2004					2005				
gender phase	1st		2nd		3rd	1st		2nd		3rd
protandrous	8%		8.5%		10%	3.5%		4.5%		7.5%
*	4.5%		4.3%			2.4%		3.7%		
protogynous	15%		14%			13%		24%		
p/SD	2004					2005				
gender phase	1st	*	2nd	*	3rd	1st	*	2nd	*	3rd
protandrous	2.0	1.0	2.0	1.2	1.7	2.5	0.9	1.6	1.1	1.2
*	2.4	1.2*	2.5			1.9	1.2*	1.5		
protogynous	3.8	1.9	4.5			1.6	1.1	1.3		

Augspurger (1983)'s modified synchronicity index was within ±10% of the synchronicity index, except for the male and female phases of protogynous trees in 2004, where it was around 0.7 instead of 0.5. Albert et al. (2001)'s modified index was about 30% (10-40%)

lower than the synchronicity index except for the above-mentioned cases, in which it was similar to it.

Vertical differences in flowering phenology within the crown (table 13) were found in two thirds of the trees in 2004 and in one fifth of the trees in 2005. The differences in 2004 were most evident in the beginning of flowering (84% of comparisons) and during the female phase (86% of comparisons). Leaves unfolded in lower crown before they did in the upper crown in 32 of 42 trees (76%, 2005). In the other trees no or just a weak spatial pattern was observed.

Table 13: Check of the hypothesis: The lower crown part is at least at two flowering phenological phases (table3) ahead of the upper part of the crown.

hypothesis holded	comparisons (2004[1])	trees[2]	gender phase in upper crown			time of comparison		
			pause	male	female	20-30.4	3-6.5	10-20.5
Yes	42	13	15	15	12	21	10	11
No	22[3]	6	8	12	2	4	10	8[3]

[1] in 2005 the hypothesis holded in nine and did not hold in 38 comparisons.

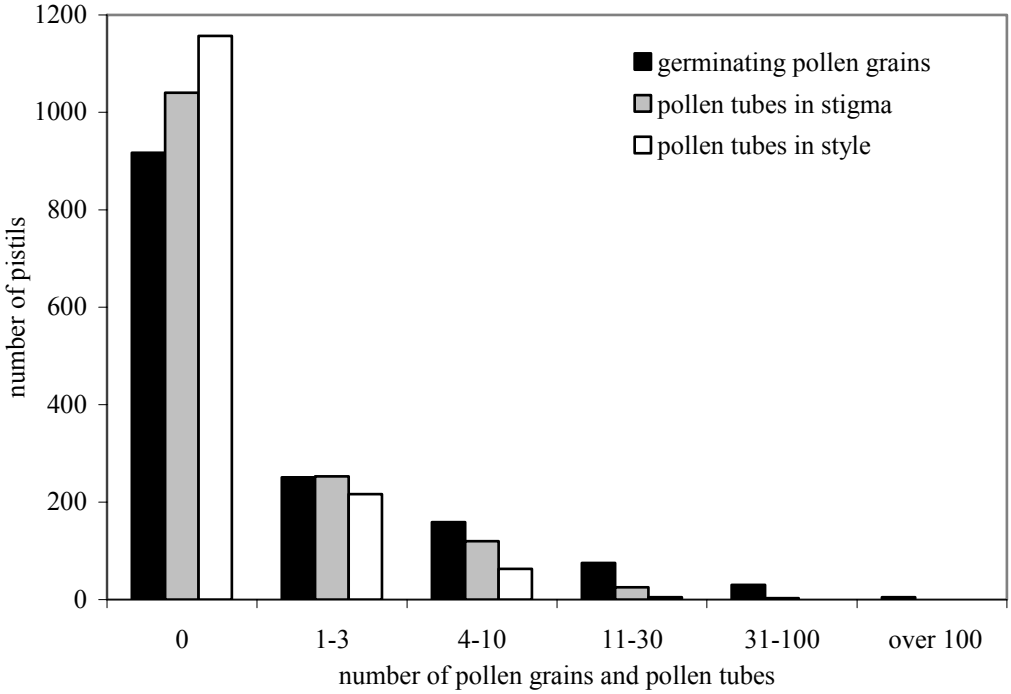
[2] other 5 trees were not consistent.

[3] in two of which upper crown was more advanced than lower crown.

Pollination and insects

Most pistils were not pollinated (figure 25a). In 4% of the probes there were more than 20 pollen grains on the stigma, and in 5% more than three pollen tubes in the style. In pistils with pollen, the median number of germinating pollen grains was four (2-9 grains were the 1st-3rd quartiles) and the median pollen tube number in the style was two (1-3 pollen tubes were the 1st-3rd quartiles). The medians of germinating pollen grains, pollen tubes in the stigma and pollen tubes in the style per probe were correlated significantly and strongly (table 14), and their ratios, after the regression slopes, were about 9:3:1 to each other, respectively.

a:



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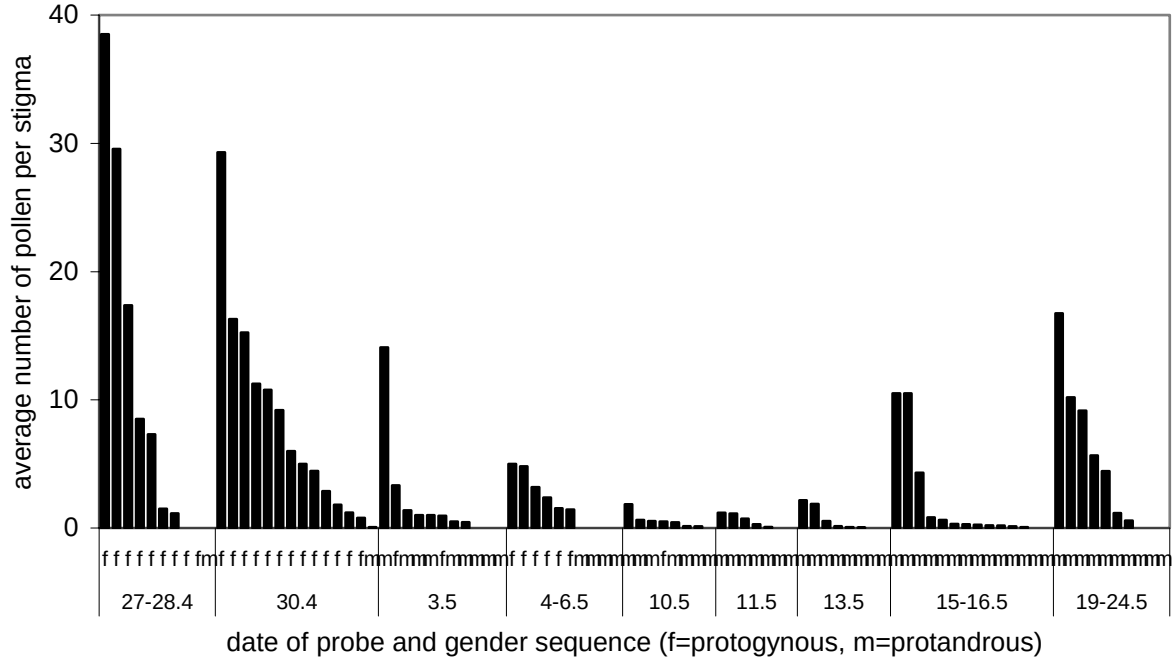


Figure 25: Pollination of *A. pseudoplatanus* (2004). The upper graph **a** presents the number of germinating pollen grains on the stigma, pollen tubes in the stigma and pollen tubes in the style for all probes. The lower graph, **b**, presents the number of germinating pollen grains after the sampling time and gender sequence (92 probes from 7 protogynous and 21 protandrous trees).

Table 14: Correlation and regression of median pollen tubes in stigma and style, and median pollen on the stigma.

correlation of medians:	Pearson product moment coefficient	regression
pollen tubes in stigma and pollen on stigma	0.85	Pollen tubes (stigma) = 0.29 · Pollen (stigma)
pollen tubes in style and pollen on stigma	0.79	Pollen tubes (style) = 0.11 · Pollen (stigma)
$p<0.0001$ for correlations and regression slopes. Regression constants p=0.4-0.5 (not significant).		

Two spatial patterns of germinating pollen grains on the stigmas were observed (referring to a subset of the probes which had germinating pollen grains and in which the spatial pattern was documented):

1. Along the stigma lobes (53 of 92 probes) – a ratio of 2:1:1 between pollen on outer, middle and inner thirds of each lobe respectively (figure 3). In probes with stigmas with many germinating pollen grains the proportions were 0.53, 0.27 and 0.21 respectively (the outer part differed significantly from the other two parts (t test $p<0.001$), middle and inner stigma did not differ significantly for all stigmas (t test, $p=0.2$) but taking only probes in which total pollen number was ≥20 they did (t test, $p<0.001$, these were 70% of the probes). in probes with total germinating pollen grains less than 50, the proportions were more scattered but their averages were similar (0.6, 0.2, 0.2 for the outer, middle and inner parts of the stigmas, respectively, the median proportion on the outer part was significantly different from the other two (Mann-Whitney medians 0.53, 0.14, 0,14 respectively, $p<0.05$).
2. Groups of pollen grains (34 of 92 probes) – 42% of grains were in groups of median size four (3-9 were 1^{st}-3^{rd} quartiles, plate 2). Large groups of pollen grains were rare (16% larger than 10, 4% larger than 30, 1.4% larger than 50). The proportion of pollen in groups increased with the total germinating pollen in the probe (regression slope 0.14, $p<0.001$, i.e. 5% increase for additional 35 grains in the probe, the largest four probes excluded) and the number of groups was positively and significantly correlated with the average pollen per probe and with the percent of stigmas with pollen in the probe (regression coefficients 0.055 and 0.67 respectively, $p(slope)<0.001$ in both, contant=0).

Vertical comparisons of pollination level showed in two of four cases a higher pollination level in lower crown and in one case a higher pollination level in crown top.

A clear temporal pattern during the flowering season prevailed. Protogynous trees had many more pollen grains per stigma than protandrous trees (figure 25b). Probes with more than five average pollen grains per stigma were found on four protogynous tree of seven (57%) and on two protandrous trees of 21 (10%). The median of averages for protandrous trees was 0.29 grains per stigma versus 4.5 for protogynous trees (Mann-Whitney rank sum test $p<0.001$). The averages and medians of germinating pollen grains and pollen tubes per probe were all significantly larger in protogynous trees as a group than in protandrous trees (Mann-Whitney rank sum tests $p<0.005$).

Thrips (*Taeniothrips inconsequens* Uzel) were numerous in the inflorescences (figure 26a). They were observed walking over all floral parts and taking off and landing, sometimes on the spread stigmas. They reproduced in the inflorescences, as at the beginning of the flowering season adults were most abundant in the probes and later on larvae were abundant (figure 26a, the number of adults before 4.5 was significantly larger than the number of adults after 4.5, Mann-Whitney rank sum test $p<0.001$). Most adult thrips were female, just a few were male. The number of larvae reached five to ten times the number of adults. No pupae were found

A significant correlation was found between the number of adult thrips per inflorescence and the number of stigmas with pollen per probe (Pearson product moment coefficient was 0.53, $p=0.028$, leaving out the point with 18 thrips). Protogynous trees were separated from protandrous trees by having more adult thrips in the inflorescences and more stigmas with pollen (figure 26b).

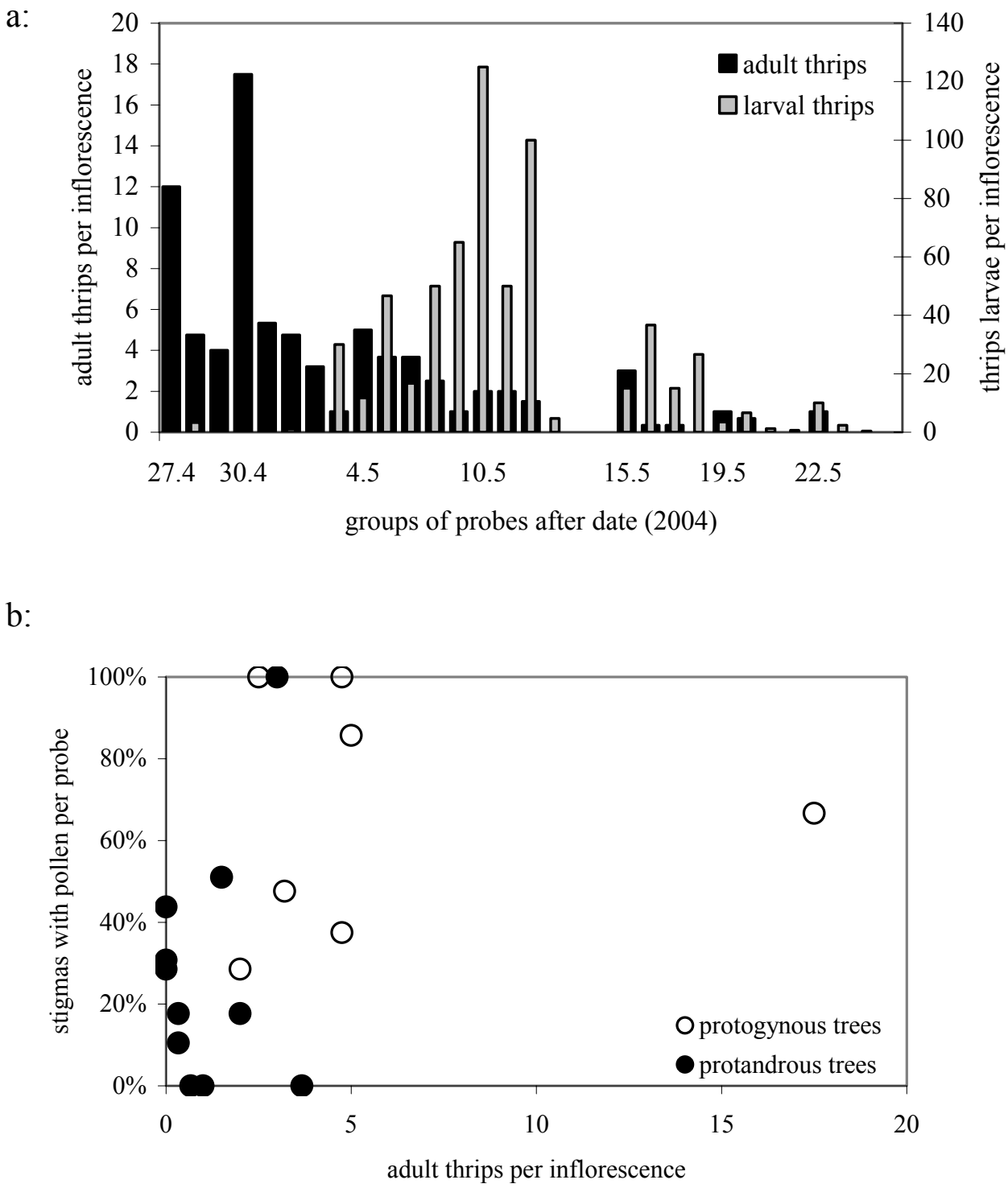


Figure 26: Thrips in the inflorescences (2004). The upper graph (**a**) presents the abundance of adult and larval thrips (*Taeniothrips inconsequens*) in the probes after date, and the lower graph (**b**) presents the correlation between the number of adult thrips and proportion of stigmas with germinating pollen per probe.

Bees and flies were rarely observed on the inflorescences. Only two *Andrena* cf. *haemorrhoa* bees and few calyptrate flies were caught, although the inflorescences were intensively inspected. These bees were common in the study area, as they were frequently observed on the earlier flowering *A. platanoides* and were also observed in large numbers in the immediate vicinity of several flowering *A. pseudoplatanus* trees but not on them (a large courting swarm of several hundred bees over an adjacent *A. platanoides* being past its anthesis). Nitidulid beetles (*Epuraea melanocephala*, mostly black) also reproduced in the inflorescences (2-3 larvae per inflorescence and 8 adults in 100 inflorescences). Chalcid wasps *Ceranisus pacuvius* Wlk. (males, Eulophidae) were found in inflorescences and were also observed with assemblages of thrips on leaves. A squirrel was observed to eat parts of inflorescences in anthesis.

Fruit

There were conspicuous differences in fruit and seed set between protogynous and protandrous trees. The former had less fruit per infructescence but more seeds per fruit than the latter. The difference in seed set was larger, so that protogynous trees also had more seed per infructescence (table 15).

Table 15: Median fruit and seed set per infructescence in protogynous and protandrous trees.

	in all infructescences (2004 / 2005)		only in the largest infructescence (2004)	
	protandrous	protogynous	protandrous	protogynous
fruit per infructescence	10.9 / 8.5	6.5 / 4.1	30.5	14
seeds per fruit	0.4 / 0.1	1.6 / 0.3	0.6	1.3
seeds per infructescence	4.1 / 0.9	10.1 / 1.1	13	18
Mann-Whitney rank sum tests between protandrous and protogynous tree groups – all p's<0.001 except for seeds per infructescence (in which p=0.007 for the averages of all infructescences and p=0.16 (not significant) for the largest infructescences).				

The seed production of protogynous trees as a group was equal to the seed production of protandrous trees as a group (table 16), although they were inferior in number (figure 22, protandrous tree included more small trees). The median seed production per protogynous tree was about three times larger than the median seed production per protandrous tree (in both years Mann-Whitney rank sum test p<0.001). This difference came to an extreme in a few

protandrous trees, which bore by far the largest fruit crops but their fruit were almost all devoid of seeds (figure 27). The proportion of fruit with three carpels per tree was significantly correlated between 2004 and 2005 (21 trees, Pearson product moment coefficient 0.79, $p<0.0001$).

Table 16: Fruit and seeds in the stand after gender sequence and in total.

study year	gender sequence	total in group		average per tree in group	
		fruit	seeds	fruit	seeds
2004	protandrous	360,000	122,000	10,600	3,600
	protogynous	95,000	125,000	7,300	9,600
	total per hectare: 350,000 fruit, 190,000 seeds				
2005	protandrous	458,000	50,000	15,800	1,700
	protogynous	113,000	46,000	10,300	4,100
	total per hectare: 360,000 fruit, 60,000 seeds				

80% of the yield (fruit and seed) in the stand was produced by 45% of the trees in 2004 and by 25% of the trees in 2005 (21 of 47 in 2004, 9 and 11 from 40, non fruiting trees excluded, for fruit and seeds respectively in 2005). One of the two protandrous trees producing the largest crops (figure 27, 27% of total in 2004, 41% of total in 2005) is the same tree in both years, the other two were checked or flowered in one year only.

The lower flowering intensity in 2005 in respect to 2004 was coupled with a smaller number of fruit producing trees, lower seed set per tree and a lower seed to fruit ratio (figure 27), although the overall fruit production is the same (table 16). The seed to fruit ratio was correlated negatively and significantly with the functional femaleness (figure 27, based on flower number in the inflorescences, Pearson product moment coefficient –0.59, $p<0.001$) and the regression between them was: Seed per fruit = $1.42 - 1.68 \cdot$ Femaleness (both $p<0.001$). The differences clearly separate protandrous from protogynous trees (figure 27).

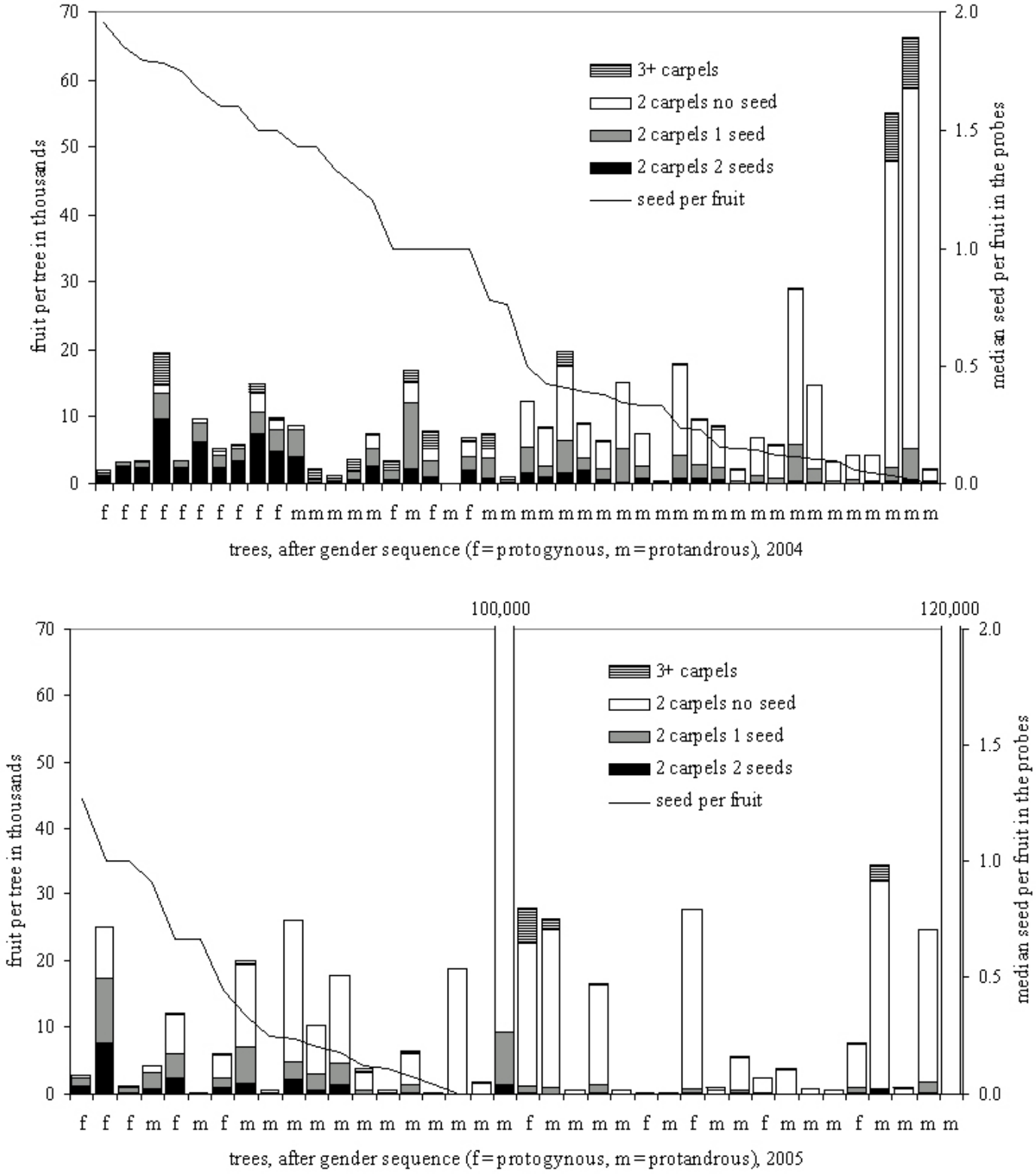


Figure 27: Fruit and seed production in 2004 and 2005. Total fruit production of individual trees denoted by their gender sequence and sorted after the median seed to fruit ratio of the inflorescences in each probe. The distribution of seed and carpel numbers in the probes is represented as different coloration of the total fruit bars. Please note that the bars for two trees in 2005 were cut to keep a common scale for the study years. Their total fruit numbers are written above the cut bars.

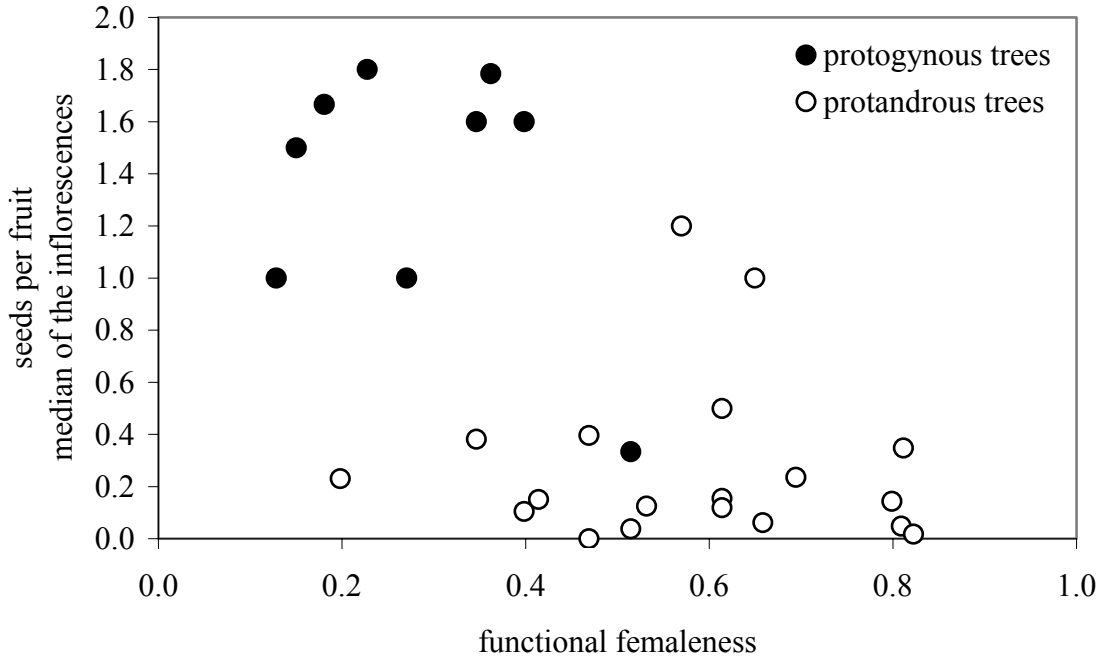


Figure 27, continued: Seed per fruit ratio in 2004 compared with the functional femaleness calculated in 2005 (figure 23).

The total number of infructescences, fruit and seeds correlated significantly in 2004 with the tree size, most strongly with the crown area (table 17). In 2005 only the number of infructescences and fruit correlated significantly with the crown area. The number of fruit was stronger correlated with tree size than the number of seeds.

Table 17: Correlations of the number of infructescences, total fruit and total seeds per tree with the tree size parameters height, stem diameter and crown area

	number per tree	tree height	stem diameter	crown area[1]
2004	infructescences	0.44 **	0.59 ***	0.68 ***
	fruit	0.32 *	0.38 *	0.55 ***
	seed	0.31 *	0.34 *	0.35 *
2005	infructescences	ns (0.08)	0.42 *	0.56 ***
	fruit	ns (0.07)	ns (0.08)	0.48 ***
	seed	ns (0.4)	ns (0.8)	ns (0.7)
ns not significant (p>0.05), * p<0.05, ** p<0.01, *** p<0.001 [1] in all comparisons crown area had the smallest p.				

The following results demonstrated that seed production per fruit was related to pollination level:

1. The seed to fruit ratio was significantly correlated with the percent of stigmas with pollen from the last probe (figure 25b, Pearson product moment coefficient 0.69, $p<0.0001$).
2. The proportion of fruit with two seeds was strongly and significantly negatively correlated with the proportion of fruit with no seeds (Pearson product moment coefficient –0.81, $p<10^{-10}$ in 2004, -0.86, $p<10^{-11}$ in 2005). The proportions of fruit with two seeds and fruit with one seed correlated strongly and significantly in 2005 but not in 2004 (Pearson product moment coefficient 0.83, $p=10^{-10}$ and $p=0.37$ respectively).
3. The proportion of seeds in fruits with two and three carpels on the same tree correlate strongly (2004, Pearson product moment coefficient 0.71, $p<10^{-7}$).
4. Partial flowering in 2005 brought with it a three-fold reduction in seed set although fruit set remained constant (table 16).

Differences in fruit and seed set within the crown:

1. Vertical: In all six comparisons upper crown had more fruit and seeds per infructescence than lower crown, in one and three comparisons respectively the differences for fruit and seeds were statistically significant.
2. Horizontal: In three of four within-crown comparisons seed to fruit ratio was significantly correlated with the distance to the next pollen-donating neighbour.
3. Temporal: An aberrant branch flowering ca. a week earlier than the rest of a protogynous tree set significantly more fruit.

Full fruit in 2004 were longer and had a larger angle between the wings of the mericarps than in 2005 (in 9 of 16 comparisons (56%) both were larger, in another four (25%) one was larger and the other one equal). These measures were not correlated per individual tree in the study years.

A fruit with two full mericarps weighed about 0.4gr, ca. 60% was seed weight and 40% wing weight (table 18). Wings of full mericarps weighed more than wings of empty mericarps in one-seeded fruits, and these weighed more than empty mericarps of empty fruit.

Table 18: Weights of fruit parts (seed and wing) in full and empty mericarps in grams. The data are ranges for the averages in five trees, and the ranges of standard deviations in parentheses.

fruit content	parts of the full mericarps		the empty mericarps
	seed	wing	
two seeds	0.09-0.13 (0.02-0.04)	0.06-0.09 (0.01)	
one seed	0.07-0.15 (0.02-0.04)	0.06-0.09 (0.01-0.02) *	0.04-0.05 (0.01-0.02) *
no seeds			0.03-0.04 (0.01) *
* These values differed significantly from each other (Mann-Whitney rank sum tests $p<0.001$)			

Tilia cordata

Gender

Flower forms found on the studied *T. cordata* trees were (figure 28, plate 7):

1. Hermaphrodite flowers.
2. Hermaphrodite flowers with a short and thin style (2-3mm at full length versus 4-5mm of normal hermaphrodite flowers).
3. Flowers with a damaged pistil in which the style was strongly curved backwards with the stigma facing the ovary. These seldom develop into fruit.
4. Male flowers of normal size with no or just a trace of a pistil.
5. Gall flowers which were small, with few functional stamens and no or just a rest of pistil.

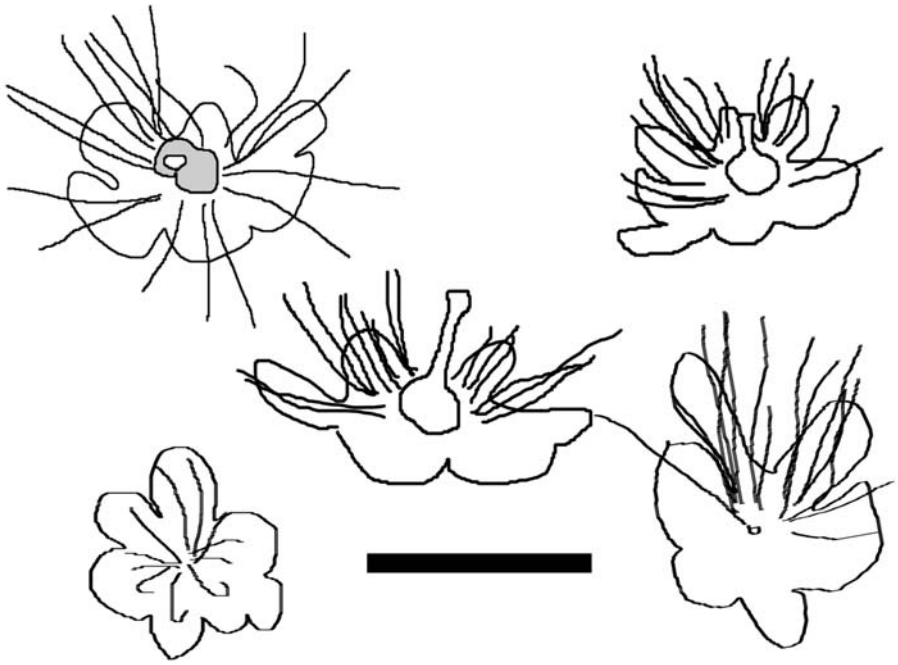


Figure 28: Five types of flowers found on *T. cordata*, drawn after photos (plate 7, stamens represented by lines, perianth coarsely outlined, the bar represents ca. 1 cm). The middle is the normal hermaphrodite flower, above it a hermaphrodite flower with a short and thin style (right) and a flower with a damaged pistil (grey), which is functionally male (left). The bottom pair consists of a male flower (right, with a minute pistil rest) and a gall flower with few stamens, which is smaller than the other types of flowers.

Hermaphrodite flowers were the most frequent form encountered (flowers with a thin style, type 2, were also considered hermaphrodite). The frequencies, or proportions in the samples,

of the three functionally male forms were found to depend in different ways on the stage of flowering, or the total anthesis, of the individual trees (figure 29, table 19). Male flowers of a normal size (with no or just a trace of pistil) were found on all trees checked. The proportion of male flowers was maximal in trees that started to flower and decreased linearily with the anthesis in the tree. Flowers with a damaged pistil were less common, and their frequency had a maximum around 50% flowering anthesis of the tree. A parabolic curve fitted the data better than a linear regression (p=0.013 versus p=0.044 for a line) and the samples with the larger proportion of such flowers also followed a curve of a similar form (e.g. the points with proportion above 3% followed the curve $0.013+0.33\cdot a - 0.31\cdot a^2$, with **a** being the total anthesis in the tree, p=0.014, a curve which similarly has its maximum at 50% ≈ $0.32\cdot a\cdot(1-a)$).

The proportions of male flowers and of flowers with a damaged pistil were correlated with each other in 2005 (Pearson product moment coefficient 0.46, p=0.002, for all 45 checks). These proportions were stronger correlated in checks from treetops (coefficient 0.56, p=0.0003), and were not significantly correlated in checks from lower parts of the crown (p=0.9), nor in 2003 (p=0.3, 10 checks). Note also that the regression curves have a similar slope of the decreasing part (-0.2, table 19).

Table 19: Summary of frequencies of the three types of male flowers and their regression to the stage of anthesis.

	frequency at crown top* (maxima)		regression to stage of anthesis (**a**)	
male flowers	7-16%	(31-36%)	0.25 - 0.21 · a	(p<0.001)
flowers with a damaged pistil	2-10%	(14-35%)	0.2 a · (1-a)	(p=0.013)
gall flowers	2 - 4%	(18-25%)	no	
* The range represents medians and maxima for 2003 and 2005 respectively.				

Gall flowers were most frequent on the first and last trees to flower (in 2005, figure 29), and were neither significantly correlated with the flowering stage in the trees (Pearson product moment, p=0.38) nor with the frequencies of male flowers and flowers with a damaged pistil (Pearson product moment, p=0.5 and p=0.3). One tree was noticeable in this respect having a high proportion of gall flowers and a low proportion of other types (9% gall flowers vs. 1.5% for the other types together). In the first tree to flower in 2003 the frequency of gall flowers in the tree top (29m) was 25% (3% with no stamens at all), and in crown bottom (19-25m) 70% (16% with no stamens at all).

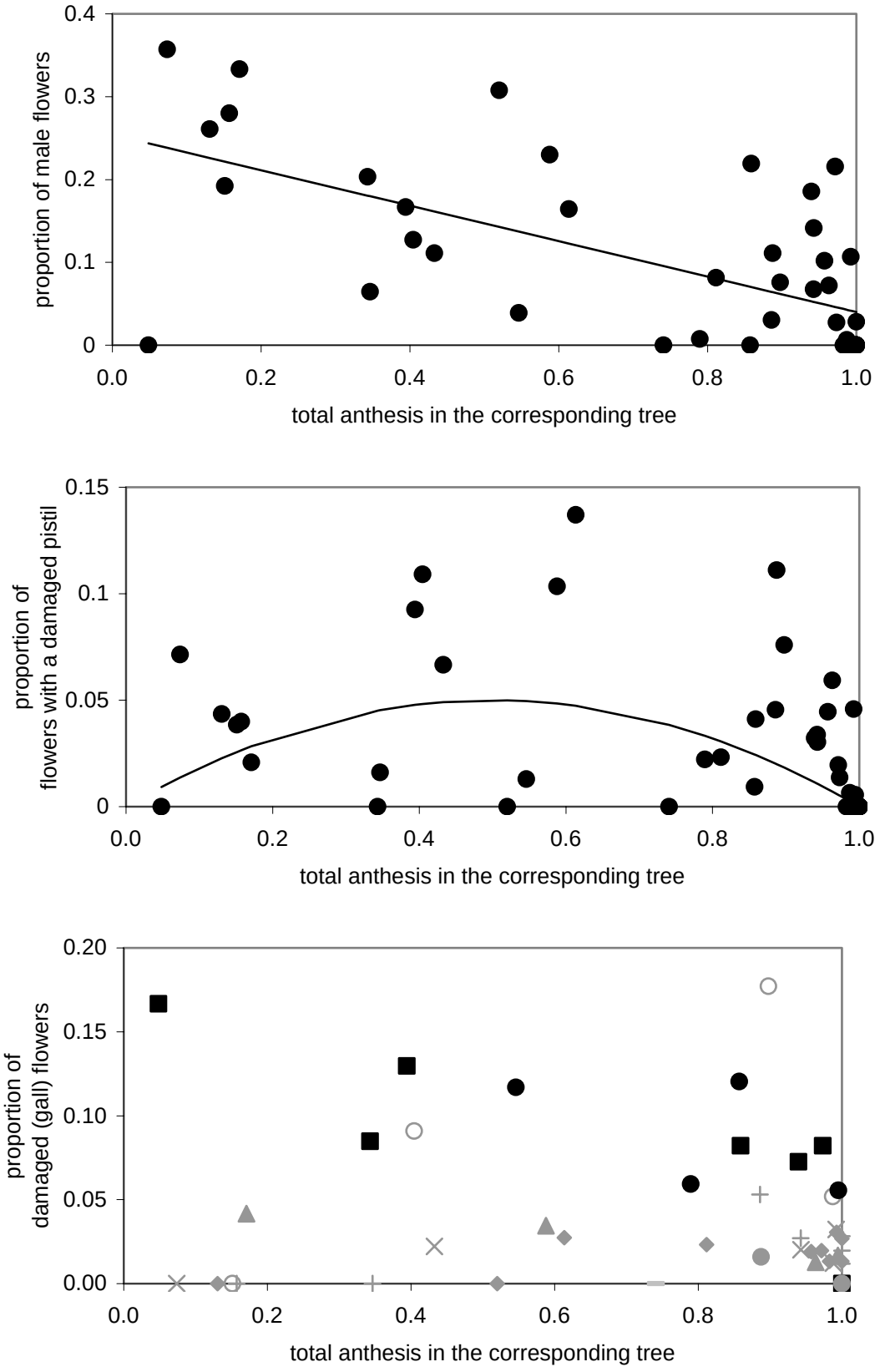


Figure 29: Frequency of flower forms other than hermaphrodite on *T. cordata*. The proportion of male flowers (up), flowers with a damaged pistil (middle) and damaged flowers (down) after the total flowering of the corresponding tree. In the upper two graphs, the regressions are depicted (the line 0.25-0.21·a and the parabola 0.2·a·(1-a), both with '**a**' being the total anthesis in the corresponding tree). In the lower graph the black rectangles denote the first tree to flower, the black circles denote the last tree to flower in the stand and the grey symbols denote probes from other trees (each tree is represented by a different symbol).

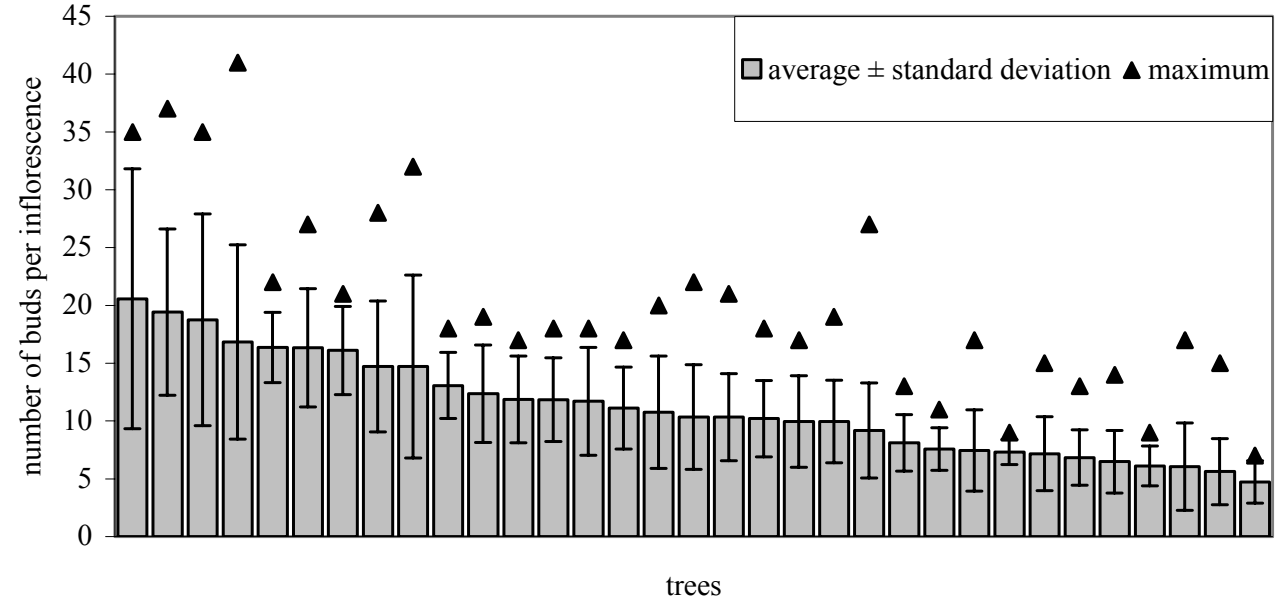
The following was observed of the gall midges and their interactions:

1. They were observed ovipositing into buds, a few days before anthesis.
2. Larvae were found within the gall flowers.
3. Damage to flowers was the sticking of the stigma to the perianth and to some anthers, or to the ovary. Its morphology was reminiscent to pistil damage in the flowers with a damaged pistil, but the pistil stayed much small and fully degenerated. The number of stamens was usually reduced.
4. Only female gall midges were caught – cf. *Dasineura tiliae* Bremi (less probable possibilities are *D. thomasiana* Kieffer, and *Macrolabis floricola* Rudow. – Netta Dorchin, personal communication).
5. Parasioid wasps were observed ovipositing into buds and opening gall flowers (*Omphale theana* Walker, relatively common, and once an *Inostemma* sp.)

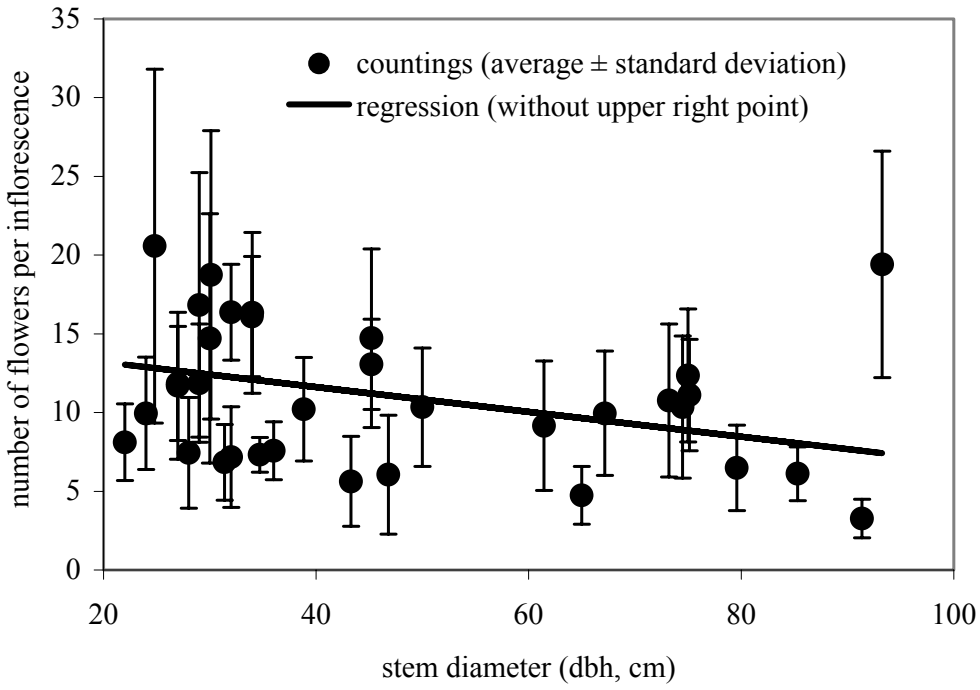
The individual trees differed much from each other in the number of flowers per inflorescence (figure 30a). Together they ranged 4-20 in average and 5-41 in maximum per tree. Trees with average inflorescence size of 15-20 flowers were no rarity. On the other end of the scale, there were trees with just a few flowers per inflorescence. The differences in inflorescence size correlated significantly and negatively with the stem diameter (Pearson product moment coefficient –0.43, p=0.013, leaving out one exceptional tree which was large and with many flowers per inflorescence). The regression was: Average flowers per inflorescence = 14.8 – 0.088 · Stem diameter (dbh, cm), p (slope) = 0.013, p (constant) < 0.001, i.e an increase of 10cm in stem diameter reduced the average flower number per inflorescence by one.

This correlation corresponded to a general change in architecture of older trees, that included a reduction in leaf, shoot and inflorescence size and a strong increase in their number and density per unit crown, as presented in table 20. In the typical, younger tree (43cm), within the sun crown, the top was less ramified and bore less leaves and inflorescences than the lower part, but inflorescences were larger and leaves were less variable in length. The shade crown was less ramified, had fewer but somewhat larger leaves and almost no inflorescences in comparison to the sun crown. The older tree had an extremely different morphology of many small twigs, with very many small leaves and very many small inflorescences.

a:



b:



c:

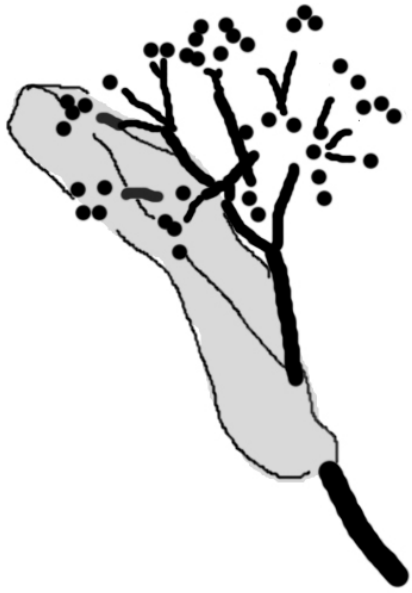


Figure 30: Number of flowers per inflorescence – variability among individual trees (**a**, 34 trees, 2004), correlation with stem diameter (**b**, the regression line is 14.8 - 0.088 · stem diameter), and the largest inflorescence found (**c**, with 41 flower buds, drawn after a photo, plate 7).

Table 20: Structural characteristics of a segment from the crown envelope, consisting of all twigs ramifying from the outer 60 cm of a branch (2003).

stem diameter	crown region	number of ramifications from main branch	leaves		inflorescences	
			number	length	number	flowers
43cm	top (29m)	8	50	6-8cm	50	10.1
	lower sun crown (22-26m)	9-13	88-104	3-10cm	73-84	4.4-7
	lower shade crown (13-20m)	2-3	13-26	3-12cm	1-3	3.3-4
91cm	top (29m)	13	ca. 1000	2-5cm	ca. 500	2.2

Vertical differences in inflorescence size within the sun crown were found however only in four of seven comparisons in 2005 (three differed significantly), in which treetop had in average ca. ten flowers per inflorescence. In the other three comparisons, in which treetop had in average ca. five flowers per inflorescence, the top and bottom of sun crown did not differ significantly in inflorescence size.

Pollen grain diameters were between 27.5-30µ (82%), 94% of the grains were within 25-30µ. Two groups of trees differed significantly in pollen diameter: Three trees had a medium diameter of 27µ whereas five trees had a medium diameter of 28.75µ (Kruskal-Wallis one way analysis of variance on ranks $p<0.001$, in a pairwise comparison all but two pairs differed with $p<0.05$, however measurement inaccuracy was ignored). Some differences were found between probes from the same tree (the greatest difference in median was 1.5µ), but these were not consistent (table 21).

Table 21: Comparisons of pollen size between flowers on the same tree

	differed($p<0.01$)	did not differ ($p>0.01$)
male versus hermaphrodite flowers	3*	3
hermaphrodites on same tree and date	0	4
hermaphrodites on same tree in different dates	2	3
* in two of the comparisons the pollen grains from the male flowers were somewhat bigger, in one somewhat smaller than the pollen grains from the hermaphrodite flowers.		

Flowering phenology

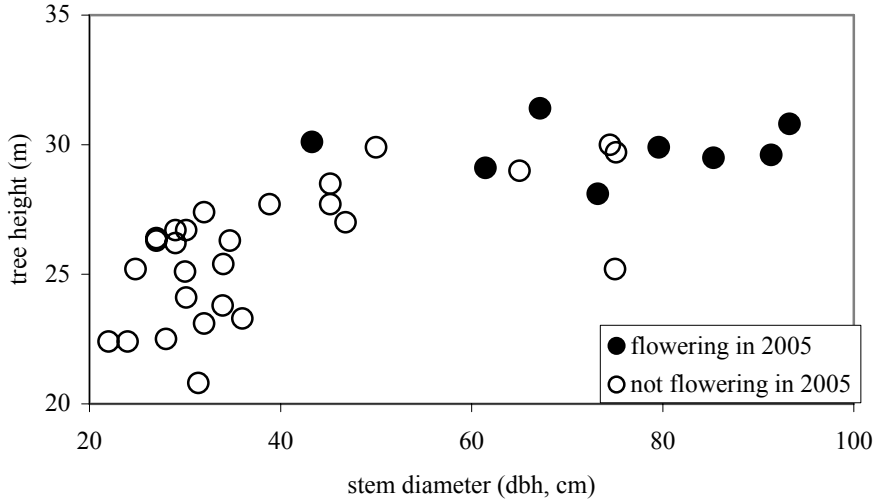
Flowering intensity differed drastically between the two main study years. Whereas in 2004 practically all canopy trees in the stand flowered (28 of 30 trees with full intensity, one tree scantly and one tree did not flower), in 2005 only three trees flowered fully, another four flowered partially, three flowered scantly and 20 trees did not flower. The trees that did flower in 2005 were the largest in the stand (figure 31a, Mann-Whitney rank sum test, $p=0.003$, $p<0.001$, $p<0.001$ for crown area, stem diameter and tree height respectively), and were all in the northern part of the plot, in which they were about a half of the *T. cordata* trees.

In all study years (2003-2005) the trees flowered almost synchronously during 2-3 weeks (last week of June to middle July), with the exception of two individual trees that usually flowered a week to two weeks before the others (flowering from the second or third week in June to the end of June or beginning of July, figure 43 in the appendix).

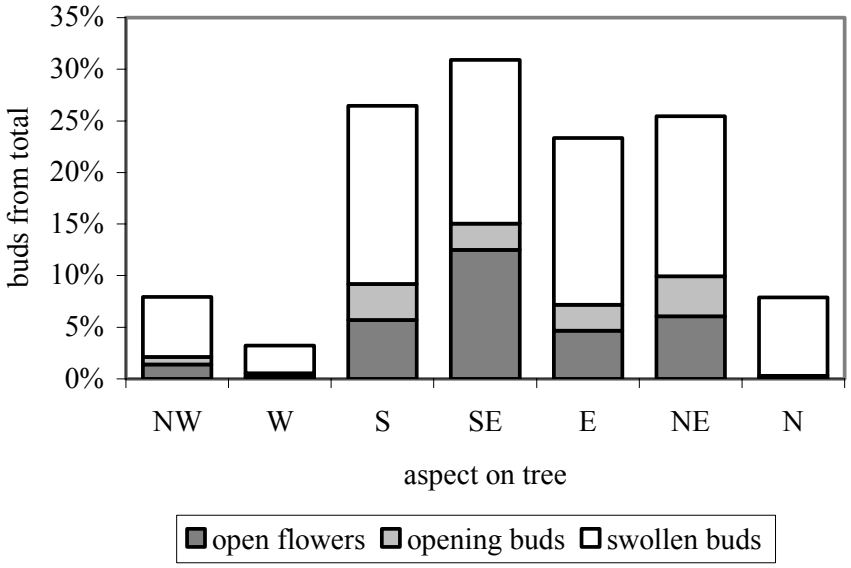
No clear vertical flowering phenological pattern was found within the crown. In 2003, in the first tree to flower, the crown top (29m) flowered after lower eastern crown (25m), in a difference of ca. 3-4 days, but a still lower (20m), western part of the crown was intermediate in its flowering stage. In another tree, a gradient in total anthesis was found from tree top (29m, no flowering), to lower parts of the crown (e.g. 28m – 9%, 26m - 25%, 20m – 29% on 20.6.2003) but with exceptional branches (e.g. at 24m with 10% flowering for the same date). In 2005, one tree was earlier flowering in lower crown (ca. 3 days), whereas in another tree no vertical difference was found.

A slight south-north difference in the crown as a whole was noted at the beginning of flowering, the southern part of the crown flowering before the northern part, (figure 31b). Clear horizontal differences were found among inflorescences along a shoot. The inflorescence at the end of the shoot (adjacent to the apical bud) flowered markedly later than the other inflorescences along the shoot (plate 7). The basal inflorescences (at the other end of the shoot) and inflorescences near the most apical one were also somewhat retarded in flowering time in respect to the middle inflorescences along the twig.

a:



b:



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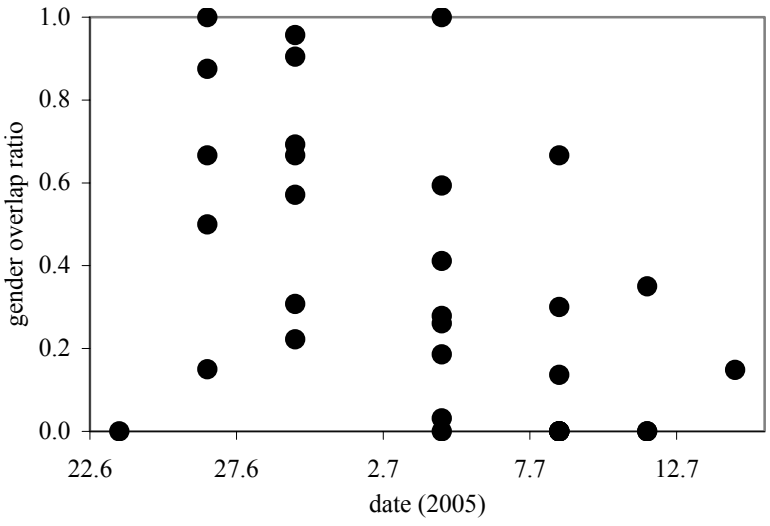

Figure 31: Phenology in *T. cordata*. **a**: Flowering intensity in 2005 and tree size. **b**: The beginning of anthesis after the aspect in the crown, average of percent of flowers with swollen buds, opening buds and open flowers on 3-5 branches at 27m (21.6.04, total 2374 buds). **c**: Overlap of male and female anthesis, index of gender overlap in 31 checks in 2005 after date. The index is equal to one when the same proportions of flowers are male and female, and is zero when all flowers flower with the same gender.

Within inflorescences, flowers came to anthesis one after the other according to their insertion in the inflorescence. They were protandrous, and each gender phase took several days (female stage seemed longer than male phase) so that a mix of flowers in male and female phase within the inflorescence was common and inflorescences with flowers in male and female anthesis simultaneously were frequently documented (plate 7). Male and female anthesis overlapped in practically all checks (figure 31c, median 60 inflorescences per check). The index of gender overlap correlated negatively and significantly with the date (Pearson product moment coefficient –0.6, p=0.0004), i.e. towards the end of flowering season the trees tended to be mainly female. In most checks (80%) the trees were more female than male. No correlation was found between the overlap index and total anthesis in the individual trees (Pearson product moment, p=0.7).

Pollination and insects

Most collected pistils did not have pollen and those that had, had mostly only a few germinating pollen grains and pollen tubes (figure 32). Pollen loads on the samples were quite small: The median numbers of germinating pollen and of pollen tubes were both zero, 2-9 grains were the range 1^{st}-3^{rd} quartiles for the non-zero stigmas. 90% of the stigmas had less than 10 germinating pollen grains (only 2.3% had 20 grains or more). 89% of the probes had less than 5 pollen tubes in the style, 16% more than 3 pollen tubes. The median of pollen tubes in pistils with pollen tubes was 3 (1^{st}-3^{rd} quartile were 2-6). The average number of germinating pollen correlated significantly with the average number of pollen tubes in the style (Pearson product moment coefficient 0.43, p=0.034, Spearman rank order coefficient 0.66, p<0.0001). The regression between them was: Average pollen tubes in style = 0.075 + 0.33 · Average germinating pollen, p(constant)=0.24, p(slope)=0.034, i.e. 3:1 germinating pollen grains to pollen tubes in style.

37% of the pollen grains on the stigmas were in groups. The average size of pollen groups on the stigma was 3.4 (median 3) and the average size of pollen tube groups was 5.1. The number of groups of pollen correlated significantly with the number of germinating pollen grains and with the number of pollen tubes in the style (Pearson product moment coefficients 0.82 and 0.86 respectively, both p<0.0001, regression slope 0.13, p<0.001 for both).

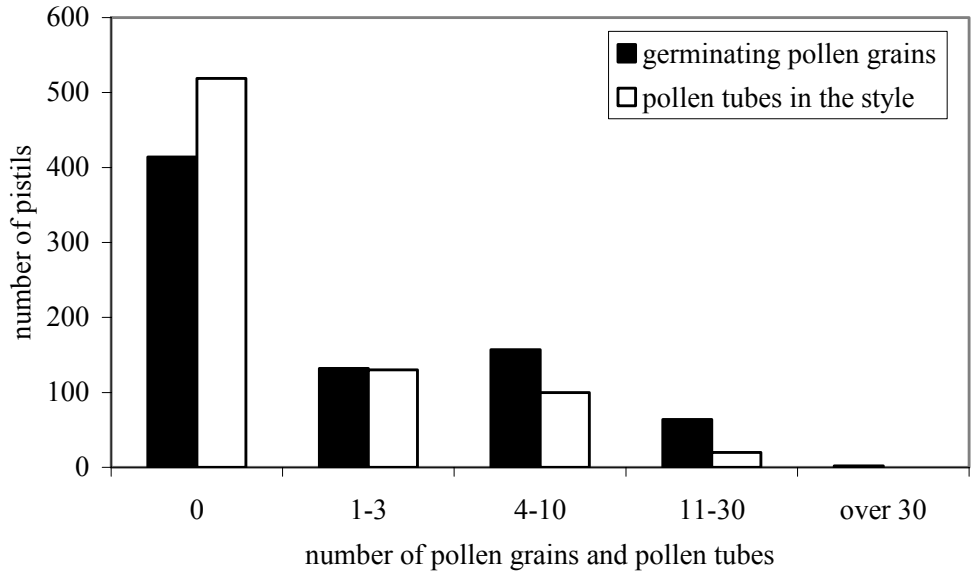

Figure 32: Number of geminating pollen grains and pollen tubes in the style for the sampled pistils.

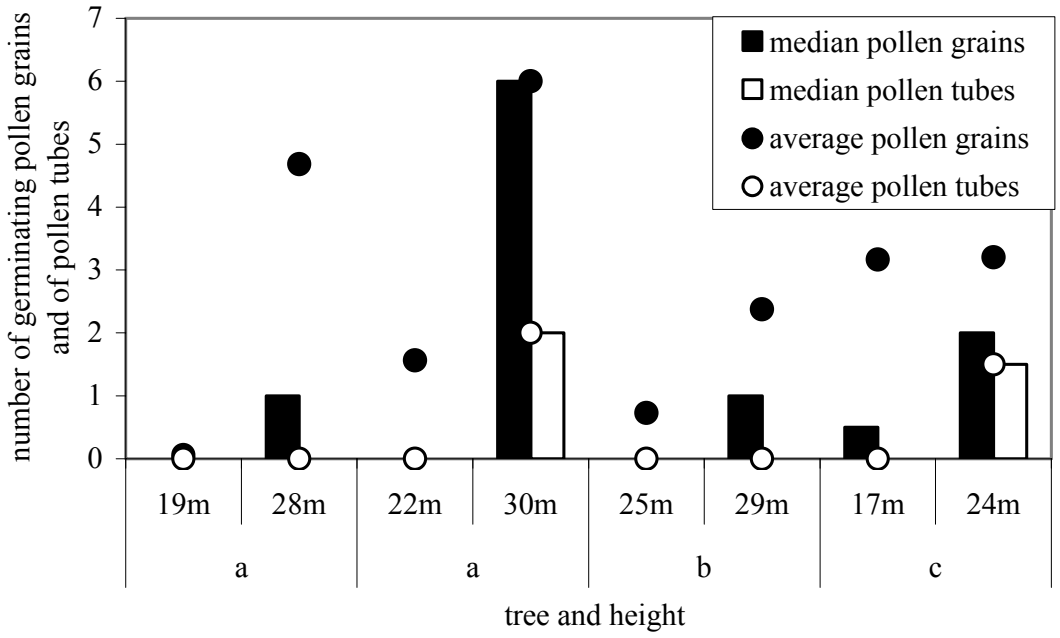

Figure 33: Height comparisons of number of germinating pollen grains and number of pollen tubes (a,b,c denote different trees). Medians represented as bulks, averages as points. Standard deviations were very large (1-4 folds of the averages).

Stigmas with unspread lobes supported pollen germination and pollen tubes were found to grow in the styles (table 22). Many checked pistils had pollen tubes in the style already at the end of male anthesis and some even before it had begun (!).

Table 22: Germinating pollen and pollen tubes in the style before female anthesis. The stages before and at male anthesis are compared (at the end of male anthesis female anthesis commences). The proportion of pistils and the average per probe of germinating pollen and pollen tubes are presented.

anthers	germinating pollen on stigma		pollen tubes in style	
	stigmas with pollen	average per probe	styles with pollen tubes	average per probe
closed	23%	0-2 (median 1)	4%	0-1 (median 0)
opened	56%	0-7 (median 2)	33%	0-5 (median 2)

Pistils in the crown top tended to be more pollinated than pistils in the crown bottom (figure 33). In the two height comparisons in the first tree, the numbers of pollen grains differed significantly between the heights (Mann-Whitney rank sum test $p=0.007$, $p<0.001$ respectively) as also did the number of pollen tubes for the second comparison (Mann-Whitney rank sum test $p<0.001$, in the first comparison both zero). The medians in the comparisons for the other two trees did not differ significantly (Mann-Whitney rank sum test $p>0.1$ in all), but the numbers in the upper probe were consistently higher than in the lower probe.

Thrips (*Thrips major*) was the most abundant insect in flowers, followed by *Epuraea melanocephala* (a nitidulid beetle), gall midge larvae (cf. *Dasineura tiliae*), *Orius minutus* (a true bug, plate 8) and several species of mostly chalcidoid wasps. Table 23 summarises the abundance of small insects in the inflorescences.

Table 23: Abundance of insects in inflorescences of *T. cordata*

group	species	average per 100 open flowers	standard deviation
thrips	*Thrips major* Uzel ca. 2/3 larvae, few *Aeolothrips melaleucus* Bagnall	32	15
beetles	mostly nitidulids (*Epuraea melanocephala* Marsham)	4	2
true bugs	*Orius minutus* L. (predated *Thrips major*)	2	5
parasitoid wasps	11 species (see below)	3	4
gall midges	larvae of cf. *Dasineura tiliae*	4	5

Chalcidoid wasps: Two species were caught during oviposition in gall midge infested buds - *Omphale theana* Wlk. (Eulophidae) and the platygastrid *Inostemma* sp. (Platygasteroidea) Further species were caught in open flowers: *Macroglenes* sp. nov. (Pteromalidae), two *Aprostocetus* spp. (Eulophidae, not determined), *Ionympha* sp. (Eulophidae, genus not known from Germany), *Pediobius metallicus* Nees (male, Eulophidae), *Omphale salicis* Hal. (Eulophidae), and also a pteromelid, an encyrtid, a trichogrammatid and two scelionids (Platygasteroidea) that were not determined. Small empidid flies (*Empis* cf. *pennipes*, after Chvala 1994) were observed feeding on nectar.

Bumblebees (*Bombus* spp.), honeybees (*Apis melifera*), and syrphid flies were observed in large numbers on flowering trees, especially on sunny days. The frequency of bumblebees changed much between the years and was low in 2003 and high in 2005.

Fruit

Fruiting was more extensive in 2004 than in 2005, as was the flowering of the trees in the stand. Most results thus refer to 2004. A few trees produced most of the fruit in the stand (figure 34a). The number of fruit per infructescence did not vary as much as the number of flowers per inflorescence, and rarely reached over five. They differed significantly (medians 10.3 and 3.1 respectively) and were correlated positively but weakly (Pearson product moment coefficient 0.42, $p=0.03$, a non-fruiting tree excluded). Their regression was: Fruit per infructescence = 1.93 + 0.12 · Flowers per inflorescence, p(slope)=0.03, p(constant)=0.005. According to this slope, eight additional flowers were needed for one additional fruit.

The largest crop was produced by the largest trees (figure 34c). Actually the trees may be separated into two groups – four (or five) as main producers and the rest as minor producers of fruit. The dichotomy is especially pronounced in respect to the crown area. All trees (but one) that bore over 50.000 fruit had a crown area around $100m^2$, whereas all trees (but one) bearing less fruit had a crown area of $40m^2$ or less. The correlation of total fruit number was the strongest and the most significant with the crown area (Pearson product moment coefficients 0.76, 0.58, 0.52 with $p<0.00001$, $p<0.002$, $p<0.006$ for crown area, stem diameter and tree height, respectively).

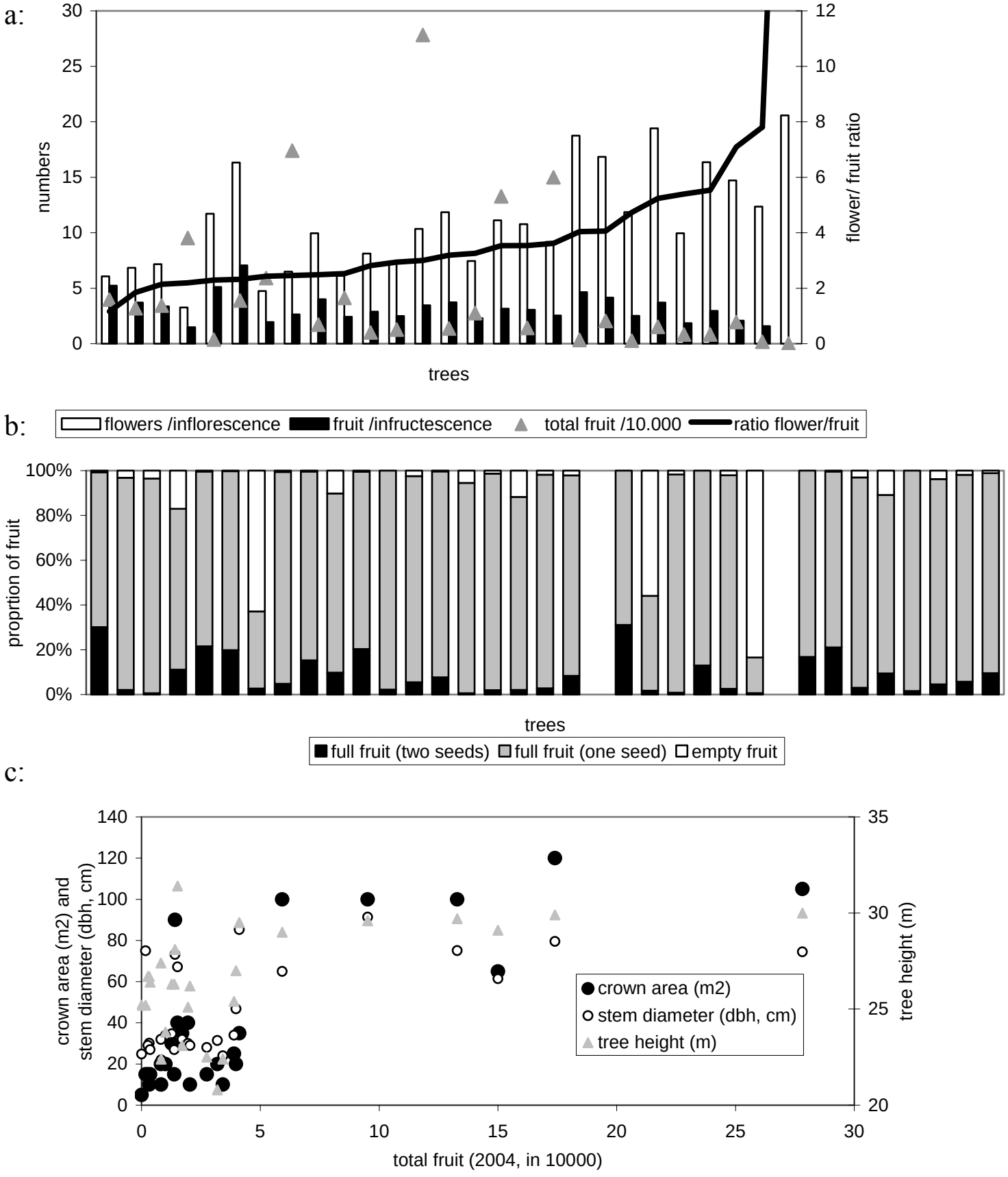

Figure 34: Fruit of *T. cordata* in the stand in 2004. **a**: Total yield and average number per infructescence, compared with the number of buds per inflorescence, and the ratio between them for 27 trees. **b**: The number of seed per fruit for 35 trees, the first 27 correspond to the trees in the upper figure, lacking data denote a missing tree and a fruitless tree. **c**: Total fruit in relation to crown area, stem diameter and tree height.

Most fruit of most trees were full and contained one seed. Still, there was some variance among the trees in the rate of empty and double seeded fruit. The percent of empty seeds was high in only three trees (9%). The proportion of two seeded fruit reached 20% in six trees (18%), all of which had less than 1% empty fruit (Pearson product moment coefficient –0.3 but p=0.09, Spearman rank order coefficient –0.48 p=0.005, both for 33 trees). The proportion of fruit with two seeds correlated with the number of fruit per infructescence (Pearson product moment coefficient 0.48, p=0.02) and the proportion of empty fruit correlated positively with the flower to fruit ratio (Pearson product moment coefficient 0.40, p=0.04). Three seeded fruit (not presented in the figure) were found on eight trees, in frequencies ranging 0.3%-1.9% per tree. For all probes together they made 0.3% of all fruit. The proportions of fruit with two and three seeds correlated strongly (Pearson product moment coefficient 0.68, p<0.0001). The ranking of the trees after the percent of empty fruit correlated negatively with their ranking after the percent of fruit with two seeds and the percent of fruit with three seeds (Spearman rank order coefficients –0.48, p=0.005 and –0.55, p<0.001 respectively).

Vertical differences within the sun crown in the number of seeds per fruit were found in two of six comparisons, in both almost all fruit in the crown top were full and almost all fruit in the crown bottom were empty. Other two comparisons showed small differences (in crown top less empty fruit and more double seeded fruit), and two comparisons did not show any difference. Nine comparisons within crown top showed no differences in the proportion of empty fruit. Fruit number per infructescence did not differ within the sun crown.

Covering of inflorescences made only in two trees out of twelve a significant difference in fruit number. In one tree exposed inflorescences produced more fruit than covered ones (t test p=0.008), whereas in the other, which was exceptional in having many more flowers per inflorescence than the other trees that were covered, the covered inflorescences produced significantly more fruit than exposed inflorescences (t test p<0.001). However, seed development was not followed till fruit ripening.

In 2005, flowering intensity, fruit production and seed production were low (figure 35). The ratio of flowers per inflorescence to fruit per infructescence ("flower/fruit ratio") was quite stable at 4-7. Two of the trees were the major fruit producers, the crop per tree for the main producers was smaller than in 2004 (figure 35a). The proportion of empty fruit reached 92%

and was high in all trees in comparison to 2004. Still, two trees had over 20% of the fruit with two seeds, and as in 2004 these were the trees with the lowest proportion of empty fruit (Pearson product moment coefficient –0.75 with p=0.02).

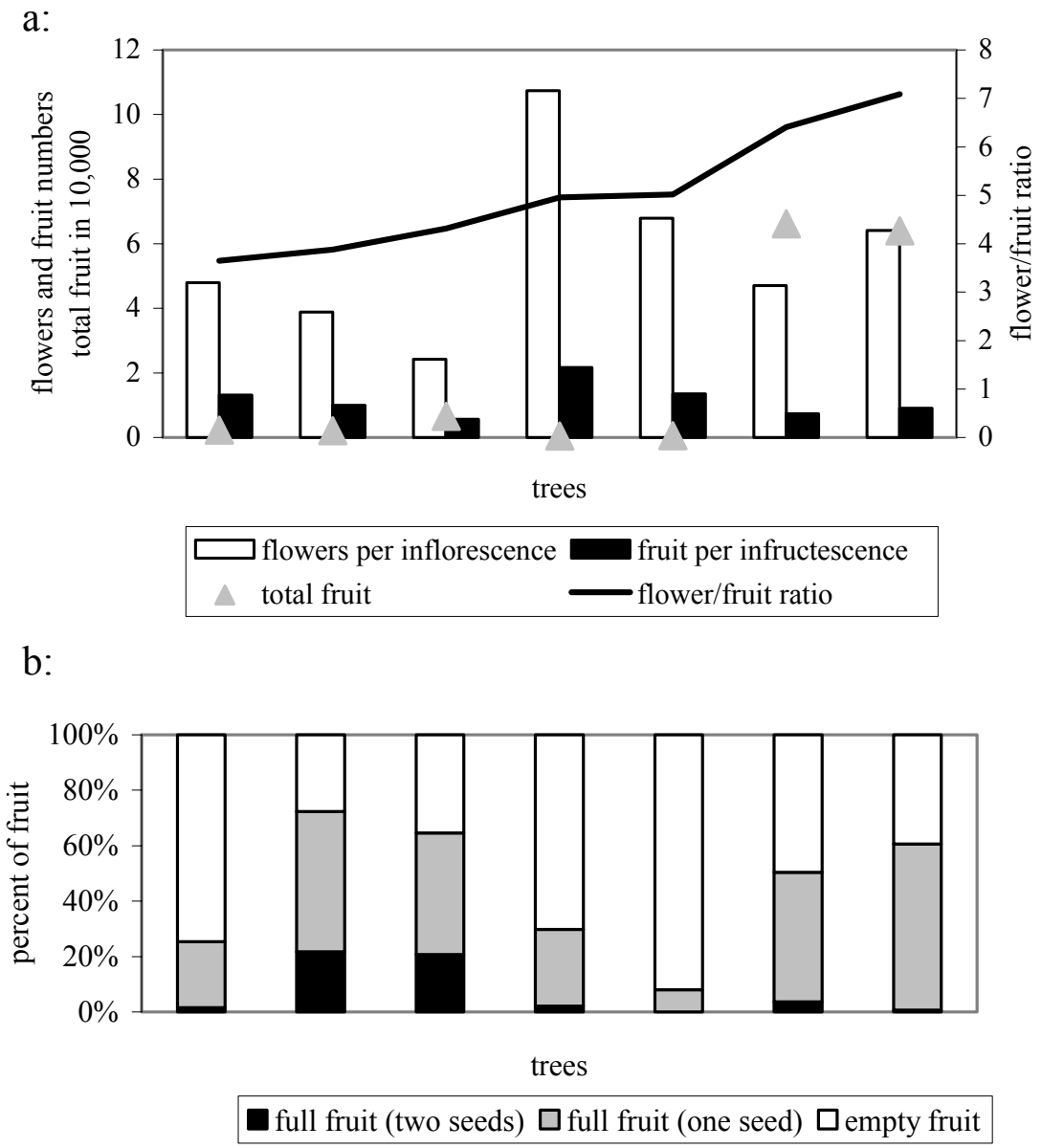

Figure 35: Fruit of *T. cordata* in the stand in 2005. **a**: Total yield and average number per infructescence, compared with the number of buds per inflorescence, and the ratio between them for seven trees. **b**: The number of seed per fruit for these trees.

Discussion

Fraxinus excelsior

The study throws a new light on the sexual system of *F. excelsior* and on its flowering phenology. I argue that *F. excelsior* is functionally dioecious, in spite of its morphological polygamy, and that this dioecy has evolved through androdioecy. The reproductive and vegetative differences between males and females are discussed. The sensitivity of the flowering phenology was demonstrated at the stand, individual tree and inflorescence levels, and its implications for *F. excelsior*'s reproduction are discussed.

Sexual system

The sex ratio (figure 7a) lies within the ratios reported in former studies (30-60% males - with no or few hermaphrodite flowers, Krzyżkiewiczówna 1928 cited in Huldén 1941 and Bredehöft 1985 respectively - and 4-40% females - the above cited in opposite order, as well as Rohmeder 1952 and Walander 2001 respectively). However the different definitions used for flower gender do not allow a direct comparison (Tal 2003) and it is not clear if gender ratio underlies a real geographical variability.

Several possible classifications of the sexual system of *F. excelsior* may be under discussion:

1. Polygamy. Wallander (2001) classified the sexual system of *F. excelsior* as polygamy, mainly due to the different morphological types of inflorescences and their composition on the trees. This has been the view since the detailed study of Schultz (1892), although different authors used simplified definitions (Darwin 1877, Krzyżkiewiczówna 1928, Rohmeder 1952).
2. Androdioecy. The family Oleaceae and the genus *Fraxinus* include a relatively high number of androdioecious species (Wallander 2001), which are otherwise rarely found among flowering plants.
3. Subdioecy is dioecy plus "imperfectly differentiated individuals" of both genders (Ross 1982) or just of male gender (i.e. andromonoecious individuals, Sakai and Weller 1999). A related term, cryptic dioecy (i.e. functional but not morphological dioecy, Mayer and Charlesworth 1991, Dunthorn 2004), was lately used to describe the sexual system of *F. ornus* (Verdú, Montilla and Pannell 2004, earlier regarded by

Dommée et al. 1999 and Verdú 2004 to be androdioecious) and may be applicable to *F. lanuginosa* (Ishida and Hiura 2002). The differences to dioecy are much a matter of taste, as already in the first uses of the "functional gender" concept it is admitted that even in a dioecious system males may have some fruit (Lloyd 1980, e.g. Webb 1979, Lloyd 1981).

The morphological variety of gender expression among the trees that is described in this study, would suggest no other definition than polygamy, as given in earlier studies (e.g. Schultz 1892, Wallander 2001). However, comparing the relative female and male fitness of the different types on a "Charnov diagram" (figure 36), a convex-concave curve typical for androdioecy results (Charnov et al. 1976). Its convexity results from the high female fitness of balanced hermaphrodites and its concavity from the low female fitness of male-biased hermaphrodite, accompanied by a relatively large loss of male fitness, which are discussed below. The difference to a typical dioecious curve depends on the transition area, which is conspicuously empty in figure 36. Indeed if balanced hermaphrodites have a low male fitness, the sexual system must be considered dioecious (e.g. Primack and McCall 1986 for *Acer rubrum*).

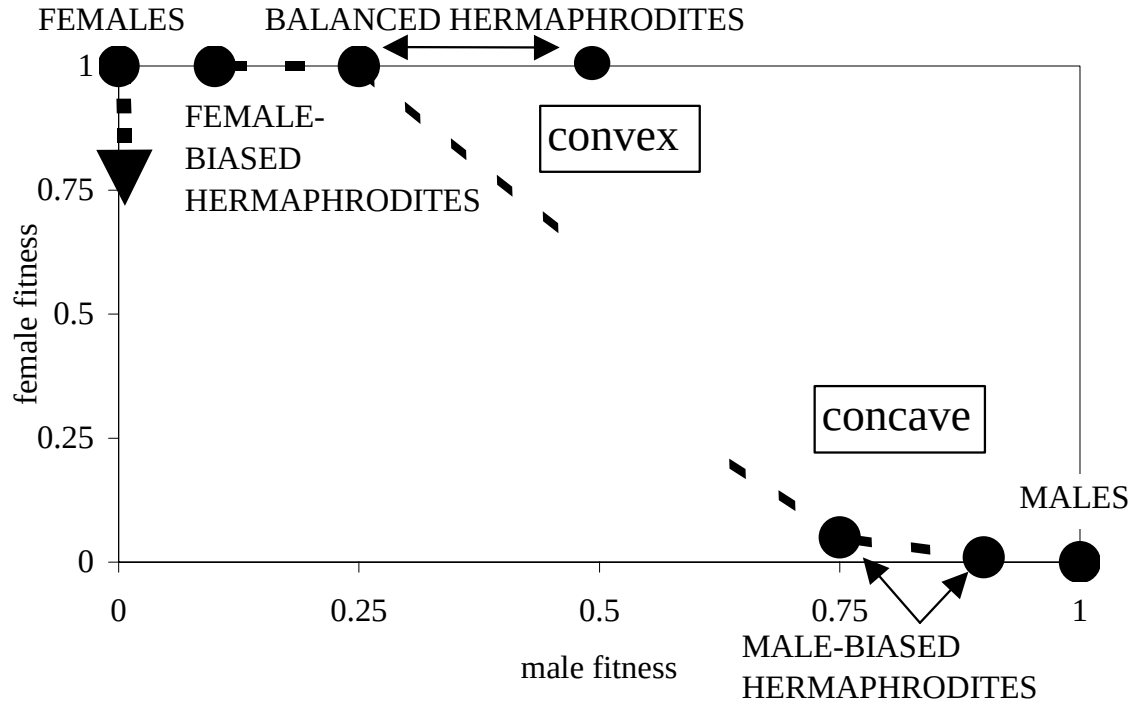

Figure 1: Female and male fitness of the gender types in *F. excelsior*, based on flower morphology, phenology and fruit crop. The double headed arrows denote the range of fitness values that correspond to balanced hermaphrodites and male-biased hermaphrodites, and the arrow for females denotes possibly reduced female fitness (see text and figures 9 and 16).

Female-biased hermaphrodites may be functionally considered female, as they produce much fruit, and a very low quantity of pollen (Darwin 1877, Binggeli and Power 1991, plate 2) of a very low vitality (Wallander 2001). Their male fitness may at most be expressed in some selfing at the very end of flowering, after a long female receptivity period.

Balanced hermaphrodites have a full female function, as they are the group with the highest yield per tree, somewhat larger than female-biased hermaphrodites and much surpassing female trees (figure 16a). The quality of the seeds was not checked, but there was no morphological indication that they are of a lesser quality. Balanced hermaphrodites probably have a low male function, as the two aspects of it are considered:

1. Outcrossing pollen. In this they are inferior to males as their anthers are smaller (Binggeli and Power 1991), their male flowering is shorter (table 7) and later, as it follows a long female flowering (figure 12), pollen vitality is lower (Wallander 2001) and have a lower seed siring success (Morand-Prieur et al. 2003).
2. Selfing pollen. This component is potentially important as anthers are very close to the stigmas, thus compensating for an inferior quantity and vitality. However, the strong protogyny leaves a long period of receptivity before the tree's own male anthesis (figure 12, table 7) and self compatibility was found to be low in most trees (results after table 8, see also Morand-Prieur et al. 2003*).* This aspect may however be important at the edge of the species' distribution or in colonisation situations (Pannell 2002, Höltken et al. 2003).

Thus, at least in a forest with a high proportion of *F. excelsior* as the one studied, selfing in balanced hermaphrodite probably plays a minor role.

The high female fitness of balanced hermaphrodites, responsible for the convexity of the upper part of the curve in figure 36, indicates that females are not much specialised. However this causes a theoretical difficulty, as the invasion of females to a hermaphrodite population is considered possible when female fitness is higher in females than in hermaphrodites (Charnov 1982). This difficulty may be explained by the following considerations:

1. Inbreeding depression may result in a lower quality of a part of the seeds of the balanced hermaphrodites, if they were sired by selfing (Darwin 1876, Charlesworth and Charlesworth 1981). The quality of seeds was not checked in this study, but strong inbreeding depression was reported by Morand-Prieur et al. 2003).

2. Females have a longer receptivity period (due to the lack of a male flowering phase) and a more gradual unfolding of the inflorescences (due to the lack of voluminous anthers, see below), two characters that may be advantageous in the long term under certain ecological conditions.
3. The limited scope of this study. Although it encompasses almost 100 trees studied over four years, it is at a great distance from being able to describe all the important effects in long-lived trees. The sample size is probably not large enough to cover the range of tree sizes in all gender types (figure 7) and four years are a short time in relation to flowering periodicity (figure 10, e.g. Primack and Stacy 1998 estimate that four to seven years is the optimal period to study a perennial herb).
4. Our ignorance of the rate and habitat in which the evolution of female trees of *F. excelsior* took place.

Male-biased hermaphrodites have a low female fitness as they produce only few fruit (figure 16a). Their male fitness is high, to judge upon anther size, but not as high as that of males, as the one male-biased hermaphrodite that produced some fruit did not flower in one of the study years (figure 10, Tal 2003), which is a clear reduction in male fitness in comparison to male trees that flower every year. Also, the large number of pistils in the other male-biased hermaphrodites, which still resulted in practically no fruit, may reduce the resources invested in the male function. These are the reasons that determine the concavity of the curve (figure 36) in it lower part.

A complication may lie in the gender inconstancy of male-hermaphrodites (suggested general sex changes, e.g. Binggeli and Power 1991 are probably misinterpretations, Wallander and Dahl, submitted, Charnov 1984). The changes observed during the study could easily accumulate over a longer period to a switch of a male-biased hermaphrodite (functionally male) to a balanced hermaphrodite (functionally female), as directly observed on one tree from 2002 to 2005. However, this complication is limited by the following findings:

1. The small number of such trees in the stand (figure 7a, comparable to Primack and McCall 1986).
2. The possible dependency on climatic factors reduces the probability of a constant change in one direction (figure 7b).
3. The low fruit production even at most female years (figure 16a).

4. The possible connection with gall mites (see below) may designate the production of female flowers of these trees as an abnormality (as in *Salix*, Freeman et al. 1980), or their general condition as stressed (Koricheva et al. 1998).

The conclusion is that *Fraxinus excelsior* is functionally dioecious, or at least subdioecious although morphologically polygamous. This situation may be typical to *Fraxinus*, as suggested by the cryptic dioecy in the seemingly androdioecious *F. ornus* (Verdú, Montilla and Pannell 2004) and the high inbreeding depression that was found in androdioecious *F. lanuginosa* (Ishida and Hiura 2002) and perhaps to some extent to Oleaceae (Vassiliadis et al. 2000, Wallander 2001).

The analysis of *F. excelsior* is also an example for the rare androdioecious pathway to dioecy. The rarity of this pathway is explained theoretically by the high male fitness required from males invading a hermaphrodite population (double in Charlesworth and Charlesworth 1978, however not necessarily if fitting the exception of a strongly decreasing male fertility function, v>>1, in Charlesworth 1984). Wallander (2001) suggests that pollination by wind may relieve this requirement by favouring specialisation in pollen production. Her suggestion is supported by my findings as discussed below.

Differences between males and females

Vegetative and reproductive differences in tree size parameters, flowering phenology and gall infestation emphasize the sexual difference between males (and male-biased hermaphrodites) and females (including in the following balanced hermaphrodites and female-biased hermaphrodites).

Male trees are larger than female trees. Rohmeder (1949, also 1967 and cited by e.g. Charlesworth and Morgan 1991, Delph 1999) showed that males are larger than female trees of the same age (ca. 50 years old, about 10% in tree height and stem diameter, about 40% in mass) and explained it by the reduction in wood mass production due to fruit mass production (1kg fruit was found to be nutritionally equivalent to 4kg wood). The studied trees in the stand are not in the same age, but still a significant, though smaller, difference was found among the larger canopy trees (figure 7c, ca. 10% in stem diameter and 3% in height). Assuming a quadratic dependency of tree mass on stem diameter and a linear dependency of tree mass on

tree height, these differences reflect a ca. 25% difference in tree mass. The larger difference in stem diameter than in tree height reflects the marked difference in twig thickness. The thicker twigs of males may relate to the larger flower number and higher flowering frequency, as the nutrient supply to the early unfolding inflorescences originates in the twig itself (Gill 1933).

Several findings support Rohmeder's (1949) hypothesis: (1) smaller canopy trees (that do not yet reproduce) are similar in size (figure 7c), (2) the negative correlation of fruit production and flowering intensity (figures 8 and 16) means that trees producing more fruit flower less often or in a lower intensity than the trees producing less fruit (the two trees excluded may well be exceptions due to the short term study). (3) Smaller fruit production on larger trees relates to smaller differences (he reports 10kg for 50 years old, 20m high avenue trees and states crops diminishes in more crowded stands, in this study most trees produced less than 10kg, results after table 9). This evidence fits better to a direct reduction of available nutrients for wood growth than to a different physiology of males and females.

Male reproductive effort may however be comparable or even surpass female reproductive effort, on the grounds:

1. Flower number – males have more flowers at inflorescence, twig and tree levels (x1½ flowers per inflorescence, Wallander 2001, x1½ -2 inflorescences per twig, observation, x1½ -2 twigs per tree, Tal 2003), and a higher flowering intensity (x1½, figure 10), making in total a factor in the range x5-9 for the flower production of male versus female trees.
2. Gall mass production inflicts males only (inflorescence galls, results after figure 7) and approaches in its weight the fruit production of female trees (x⅓-½ for trees of comparable size, and produced every year thus x1½-2, resulting in a total factor of ½-1). However if their chemical composition is similar to wood than their cost to the tree is only ¼ of the cost of the same weight of fruit (Rohmeder 1949).
3. The green fruit wings may be supplying a part of the energy to the developing fruit and decrease their costs to the tree (Bazzaz et al. 1979 in winged fruit of other temperate trees, e.g. *Acer* spp., Eisenhut 1957 for *Tilia* bracts, Cipollini and Levey 1991 with solar radiation level from Stoutjesdijk and Barkman 1992).

Male trees seem to be more specialised than female trees. Floral morphology, inflorescence morphology, inflorescence phenology and flowering phenology of the trees were all found to

be further derived in male trees than in female trees in respect to the ancestral hermaphrodite condition. This might be explained by sexual selection being stronger in males due to the anemophilous pollination mode (Willson and Burley 1984, Burd and Allen 1988, Willson 1994, Wallander 2001). In wind pollinated plants, the reproductive opportunities of males are limited mainly by their pollen production whereas the reproductive opportunities of females are limited mainly by their available nutrients and by fruit dispersal, which reaches in *F. excelsior* not much further than the mother tree in a stand (Heuertz et al. 2003), and not by pollen capture abilities. Differently formulated, anemophily implies an approximately linear male gain curve but a saturating female gain curve (Charnov 1982). The increase in flower number at different levels (see above) indicates that male specialisation is basically on pollen number. Further evidence is possibly the larger number of twigs on male twigs, reflected by the greater difference in stem diameter than in tree height (figure 7c, Rohmeder 1949). More twigs support more leaves that assimilate more nutrients that support the specialisation. Pollen size in males was somewhat smaller but not significantly different than in hermaphrodites, but the four trees with largest pollen were hermaphrodite. Pollen size was much more variable among the trees than was found by Wallander (2001). As reduction of pollen size may also increase pollen number (Cruden 2000), it may be interesting to study the variability of pollen size among and within trees more thoroughly.

A high synchrony of individual trees combined with a strong protogyny at tree level, may promote male specialisation by increasing the advantage of males invading a hermaphrodite population – males simply do not have to wait to the end of the female phase (Thomson et al. 1989). This suggestion is supported by the actually earlier unfolding of inflorescences on male trees (see below). A generalisation may follow, that a protogynous species with a long female phase, in which individual are synchronised, will tend to develop male individuals (i.e. become androdioecious), overcoming the "double male fitness" theoretical requirement (Charlesworth 1984, Wallander 2001) by flowering phenological means and not necessarily primarily through its morphology.

Why do gall mites infest massively only male trees? The infestation of male trees may result from: 1. Their constancy of flowering. Non-flowering years of females may disable mites to build a large population (Sabelis and Bruin 1996). Males may even change gender in reaction to a massive mite infestation (a tendency observed in two trees, but needs a longer study to substantiate). 2. Possibly imitation of a female hormone by the gall mites (Royalty and

Perring 1996) as the ontogeny of the galls on a twig resembles that of an infructescence (plate 8, Tal 2003) and as the capacity of male trees to produce hermaphrodite flowers is testified by a half of the male trees that produce few hermaphrodite flowers (figure 7a). Alternatively a physiological difference may exist between males and females that makes males more susceptible to infestation (Westfal et al. 1996, Årgen et al. 1999).

The cost of the galls is difficult to assess as their production may involve direct and indirect (e.g. physiological) effects (Royalty and Perring 1996). The weight of galls is in the order of magnitude of fruit production (which does represent a considerable load on females, Rohmeder 1949), but their chemical composition, which was not studied, may be less costly than fruit. On the other hand infestation is yearly and commonly massive (Wardle 1961, Castagnoli 1996) and the infested trees in the stand did seem weaker (thinner twigs, low flowering intensity, commonly outcrowded by neighbouring trees, Tal 2003, however these stress indicators could also be conditional to infestation, Westphal et al. 1996, but see Koricheva et al. 1998). Gall production probably does not directly damage pollen production, as it occurs after male anthesis, but it may lower the available resources on the twig level for the pollen production in the next year (as flowering precedes the unfolding of leaves and thus probably relies on stored nutritients at twig level, Gill 1933, also Burd and Head 1992).

What is the effect of gall mite infestation on the sexual system? How can the male specialisation in *F. excelsior* be reconciled with the expectation that male biased herbivory should promote female specialisation (Ashman 2002)? Possible answers are: (1) Galls may be irrelevant to the sexual system if their production has a negligible cost. (2) *F. excelsior* may actually be female specialised in traits not studied here. However male specialisation was exemplified in several morphological and phenological traits. (3) The gall mites may promote the male specialisation, as suggested for gall mites on leaves of *Acer opalus* by Verdú, García-Fayos and Gleiser (2004), through an "arms race" between males and gall mites (see Lindquist and Oldfield 1996 for the mites' perspective). In *F. excelsior* two concrete scenarios may be envisioned for such an "arms race": (1) A male adaptation to compensate for resources drawn from the twigs by gall building is utilized to an increased pollen production in uninfested individuals. (2) If mites exploit the effects of female hormones (see above), a reduction of their affect (i.e. male specialisation) may be advantageous.

Plasticity in gender determination? Several indications for plasticity in gender determination were observed: At stand level - more femaleness at years with warmer early spring (figure 7b), at tree level in male-biased hermaphrodites - more hermaphrodite flowers in lower crown (Tal 2003), at inflorescence level - embryonic flowers were more often bisexual than adult flowers, and apical flowers in the inflorescence (exposed first) were more bisexual than the rest of the flowers in the inflorescences (in male-biased hermaphrodites more female, Tal 2003, and in female-biased hermaphrodites more male, observation in 2005). The latter finding suggests that flower gender is controlled by weather at inflorescence level. The cessation of stamen and pistil development in different types of females and males may depend on an interplay of flower and inflorescence development with temperature and physiological factors (Chailakhyan 1979, Leins et al. 1988, Coen and Meyerowitz 1991, Thompson 1991, Pigliucci 1996, West-Eberhard 2003, Mitchell and Diggle 2005). Variability among trees, arising from different geographical origins (Wayne and Bazzaz 1991) and different genetic constitution (Heuertz et al. 2001, Morand et al. 2002, Petit et al. 2003, see however Boshier and Stewart 2005) may be expressed directly in different susceptibilities to the complex factors determining floral development (Taiz and Zeiger 2000, Lehrbuch der Botanik für Hochschulen 2002) or indirectly by their influence on the vegetative climatic adaptations of individual trees (Körner in press), affecting their reaction in reproductive characters. The correlation between gender traits and genetic variability is studied for the trees in the stand (Parolin et al. in press). A detailed ontogenetic study is needed to clarify the exact processes of gender determination in *F. excelsior*, possibly exploiting the experimental manipulation of covering twigs with paper bags (figure 14b).

Flowering phenology, climate and reproduction

Stand and tree levels

The flowering intensity and fruit production were more or less constant over the four study years (figures 5 and 6). This is different from the two years' cycle reported for *F. excelsior* in other stands (Gardner 1977, Tapper 1992a, b and 1996, Wallander 2001) and in particular does not present a masting pattern. Males flowered constantly with maximal intensity, contrasting fluctuating male flowering intensity reported by Wallander (2001) and Wallander and Dahl (submitted). Females flowering in low intensity every two-three years and the negative correlation of their flowering intensity with fruit production suggest resource

limitation of individual trees (Gardner 1977) but a masting pattern at the population level did not arise due to the lack of synchronisation among the trees (Lalonde and Roitberg 1992). A constant male flowering intensity relieves females from the risk of lacking pollination, thus removing a potential advantage of synchronous flowering (Smith et al. 1990). Synchrony of fruit production was attributed by Tapper (1992a) to satiation of frugivorous moths, which do not cause much damage here. Here gall infestation seems to be the main arthropod disturbance to reproduction, and synchrony among trees is not required (in the sense of ultimate purpose) to collapse gall mite populations, as they cannot massively disperse to long distances (Sabelis and Bruin 1996). As synchrony among masting trees depends both on clear climatic cues and on predation pressure (Janzen 1971) a lack of them may explain the asynchrony of fruiting in this stand.

Direct frost damage to the flowers was the only factor found to somewhat decrease fruit production. The time of flowering of *F. excelsior* is not optimal in this respect, as frost still commonly occurs in April. However, the probability for a long frost period is already below 10% in March (see appendix, after table 29) and frost damage was avoided or reduced by floral phenological adaptations at inflorescence level (see below).

The synchronisation of flowering duration among the trees was low in 2002 and high in the other years, especially in 2005 (figure 13). Low synchronisation may limit the number of possible mating partners and also the variability of the progeny (Primack 1985, for 2002 - Tal 2003) and especially increase the difference in male success between the trees (Stephenson and Bertin 1983). The synchrony between trees of reciprocal gender was a bit higher than the synchrony of all trees together, but this is probably an artefact of the dependency of the index on the number of trees, which was lower in the former due to the limited number of tree pairs.

The five measures used to quantify synchrony showed the same qualitative differences. Primack's (1980) synchronicity index has the advantage of relating directly to the overlap in flowering time, in contrast to the duration to deviation measure that somewhat missed the difference between 2003 and 2004. The proposed step measure improves the synchronicity index in that it is independent of the number of plants and being somewhat intuitive, but has the disadvantages of being meaningful only when flowering durations are not too variable and is inapplicable to measure synchrony of plants of reciprocal gender only. The two modifications of the synchronicity index of Augspurger (1983) and of Albert et al. (2001) are

in their merits and weakness similar to the original index of Primack. They deliver different spectra of values for the data presented, and choosing between them is probably a matter of taste.

Flowering duration fluctuated strongly among the study years (figures 11 and 12). The climatic factors governing this variation seem to be the timing of cold events in the early spring – end of winter and cold interruptions during flowering period (appendix, table 29). The start of flowering seems to be at the beginning of warm phases (after a strong increase in minimal daily temperature, not necessarily in a sunny period, appendix, figure 43, and similar to Wallander 2001), and flowering duration seems to lengthen when flowering is interrupted by cold periods (appendix, figure 43 and table 29).

The main period of flowering, however, was remarkably constant in the study years (figure 11). The study years covered most of the range of weather variability in the last 30 years, in terms of temperature sums (appendix), but years with an exceptionally late winter end did not occur (5 in the last 33 years). 2006 is such a year with an exceptionally late winter end, and *F. excelsior*'s main flowering duration was delayed and shortened in respect to the study years.

Starting dates are commonly used to reflect phenological changes resulting from climate change (e.g. Fitter and Fitter 2002). *F. excelsior* is exceptional in not starting flowering earlier during the last 30 years (van Vliet et al. 2002). It may be so due to the difficulty to observe the inception of flowering, reflected in the total discordance of the data here with the DWD data for the same region (appendix). However, as the climatic effects on *F. excelsior* are especially conspicuous, this species should be sensitive enough to react to climate change. This species also demonstrates that climatic changes that affect the flowering process may depend on the way winter changes into spring and not necessarily on the averages and sums that are commonly used to measure them.

The median duration of main flowering per tree in the study years did not differ much, neither among years nor between genders (table 7). Male and female trees did not differ in starting times, nor in the duration of flowering (table 7, as in Wallander 2001). Individual trees were to some extent consistent in the time of flowering commencement, reflected by the significant correlation of their relative rank between years (after table 7), however the ranking of the trees in 2005 and 2003 is not very reliable due to flowering characteristics. Individual

differences in flowering commencement may be rooted in genetic differences, reflecting the plasticity of genetic mechanisms determining them and relating to different origins of the trees and their geographical variability (Primack and Kang 1989, Heuertz et al. 2001, Morand et al. 2002, Petit et al. 2003, West-Eberhard 2003, Komeda 2004, Stinchcombe et al. 2004). The correlation between phenological traits and genetic variability is studied for the trees in the stand (Parolin et al. in press).

Early flowering trees flowered longer (table 6), however mainly due to lengthening of the initial flowering phase. This may be due to lower temperatures that cause slower development (Taiz and Zeiger 2000, Lehrbuch der Botanik für Hochschulen 2002). The initial phase followed conspicuously the pattern down-upwards and within-outwards in the crown (acropetalous and centrifugal) which may relate to the "physiological awakening" of the trees in early spring. However inflorescence unfolding may result directly from local cambial activity in the twigs (Gill 1933 and references therein) and the factors influencing the commencement of this activity are not clear. *F. excelsior* does not have sap flow in early spring (Essiamah 1980 and 1982), and this "physiological awakening" in trees is probably a part of the not understood region of xylem physiology (Tyree and Zimmermann 2002, Zimmermann et al. 2004, see species comparison below). It may relate to a transport of water in a small amount or of hormones that are just enough to initiate the flowering process (Stephan Mayr, personal communication).

Inflorescence level

Differences of inflorescence gender types in respect to the recent work of Wallander (2001) probably result from the different methodology and stand maturity and not from a difference in biology. The splitting of the male I and female categories of Wallander (2001) reflects a higher ability to scrutinize and to typify the trees (respectively) using the crane. The bringing together of her male II and hermaphrodite III (to male-biased hermaphrodite) and hermaphrodite I and II (to balanced hermaphrodites) are due to difficulties to distinguish them on the scale of the whole tree (the former due to annual changes in gender expression, the latter due to the large dimensions of the trees).

Inflorescence phenology in *F. excelsior* takes different courses in males and females, which show adaptations (in respect to the ancestral hermaphrodite and protogynous inflorescences,

Wallander 2001) to climatic factors and reflect gender specialisation in relation to wind pollination. In females, from balanced hermaphrodite over female-biased hermaphrodite to female inflorescences, inflorescence form at the beginning of anthesis changes from globular to oblong due to the decreasing anther volume (plate 3). The phenological implication of this geometrical difference is that a large number of stigmas are exposed immediately as balanced hermaphrodites buds open, whereas only a few stigmas are exposed as female buds open, and the exposition of stigmas is more gradual (plates 2 and 3). The stigmas in the former are not receptive at bud opening and become receptive later and together. In contrast, stigmas of female inflorescence are receptive as they are exposed and further exposition occurs stepwise. The result is a prolonged female anthesis period and a higher redundancy against frost at the beginning of flowering in female inflorescences. These differences may be due to different grades of adaptation against frost damage, but may also be only a side effect of the different origins of the trees (Heuertz et al. 2001, Morand et al. 2002, Petit et al. 2003).

In males, the "waiting phase" of the inflorescences (results after figure 13) seems to parallel the missing female flowering (Tal 2003), and is preceded by inflorescence unfolding. It seems surprising, that male inflorescences retain the ancestral protogynous rhythm because male competition underlines the importance of being the first to flower, when females are receptive (Stephenson and Bertin 1983). As the actual commencement of anthesis does not differ between males and females (results after table 7), it is concluded that male inflorescences actually unfold one to two weeks earlier than the (ancestral) hermaphrodite inflorescences. (This may explain the female deficiency of male-biased hermaphrodites – they flower too early for their female function, that is thus stronger damaged.) Male inflorescences unfold earlier but their lengthening is postponed and often misses altogether. They take so the opposite way to evade frost damage – instead of redundancy they wait in a protected state just before anthesis. Actual anthesis is then exogenous controlled by sun irradiance (figure 14c) and not endogenous as in female trees (figure 14a).

The easy experimental manipulation of inflorescence phenology illustrates both the dependency of frost damage on inflorescence length (figure 14b) and the high susceptibility of inflorescence phenology to microclimate. It also shows that microclimatic differences are more significant on a small scale to organisms than on a large scale in early spring (see also Jackson 1966, Stoutjesdijk and Barkman 1992, Geiger et al. 1995, Tal et al. in press).

Reproduction

The pollination mode is anemophily and pollen release occurs probably both under weak winds (as observed on fruiting patterns on adjacent trees in special spatial constellations) and as a result of sudden twig movement (due to a strong wind gust, branch clashing or a bird picking, observation). Birds picking in the inflorescences for insects (Hudde 1993) serve the tree as cleaners, and may as well act as secondary pollinators as a bird with pollen was caught on a female tree. When bad weather leaves *F. excelsior* inflorescences as a main food source and impedes pollen flight, their contribution may be worth mentioning. Blue tits have been reported as being able to pollinate temperate flowers (Búrquez 1989) but the large number of flowers per tree probably cannot be effectively bird pollinated. The stamens on the functionally female balanced hermaphrodites may be interpreted as serving the attraction of bees and flies for some insect pollination (Wallander 2001). The inflorescence structure is most similar to *Salix* (e.g. *S. caprea*), a genus in which return to entomophily is reported (Meeuse 1978). Pollination level is high and pollen tube attrition is intensive (figure 15, table 8, Honig et al. 1992).

The yield of the stand is similar to the maximal yields reported by Gardner (1977) and Tapper (1996), and the crop per tree is similar to Rohmeder (1949, also cited in Wardle 1961). The relation of maximal crop to crown area but not to tree height or stem diameter shows the importance of canopy space conquest (Frech et al. 2003, Roloff 2004) and of this size parameter, but may however be an artefact of the similar counting methods.

The frequencies of empty fruit and of fruit with two seeds are intermediate between Wardle (1959, more empty fruit, less double seeded) and Huldén (1941, more double and three seeded fruit) and similar to Gardner (1977). The phenomenon reported by Tapper (1992a), of a year with mostly empty fruit preceding a mast year was not observed. The trees presented different grades of self-compatibility, but a study of seeds and seedlings (e.g. Acatay 1938) is needed before final conclusions may be reached. Fruit amount per infructescence was very variable within and between trees, probably reflecting differences in pollination and nutrition. If there are somatic differences within individual trees (Whitham and Slobodchikoff 1981, Klekowski et al. 1985 and see appendix) as indicated by initial results of Parolin et al. (in press) fruit amount may also reflect it.

Acer platanoides

Flowering phenology

The flowering of *A. platanoides* (accompanied with flushing, as the inflorescences are in terminal buds) preceded the unfolding of leaves of the other tree species in the forest in about two weeks (figure 43), causing flowering trees to be more conspicuous in the forest than they were if they had flowered later. *A. platanoides* unfolds its leaves early in respect to tree species with similar wood anatomy (Lechowicz 1984 and 1995) and is thus potentially at a higher risk of frost damage. Non-flowering trees seemed to flush later than flowering trees in 2004 and 2005, but this observation was not quantified. Flowering intensity fluctuated between full flowering in 2004 and almost no flowering in 2005 (figure 5, followed by a full flowering in 2006), the latter of which was fully devoured by nitidulid beetles and aphids. It may be that due to the small supply of flowers herbivore damage was more concentrated.

The beginning of flowering is closely connected with inflorescence lengthening (figures 18 and 19), which is intimately connected with the gender presentation sequence (Haas 1933). The observation that the first flowers leans in the opening bud towards south (plate 6) is somewhat reminiscent to male anthesis in *F. excelsior* (figure 14c, plate 3), demonstrating the importance of microclimate and may have a similar effect to heliotropism of herbs in cold habitats (Kevan 1975, Stanton and Galen 1989). Interruption of the sunny periods corresponded with gender phase changes, as reported by Grube (1988). The pause between the first male phase and the female phase contrasted with a partial overlap in the second gender phase, similar to the reports of Vogler (1906), Haas (1933) and Svobodová (1973). Flowering duration is also similar to these studies.

The flower phenological pattern in *A. platanoides* – anthesis from crown bottom upwards and from the inner crown outwards - is conspicuously superposed on the complex duodichogamous gender sequence (figures 18 and 19, Haas 1933, Stout 1938). All three gender phases unfolded in this manner, that was especially evident in the middle crown (figure 19). This pattern was not found in the literature. The gradual ascent of sap in early spring may be responsible for this pattern (Huber 1956, Essiamah 1982, Tyree and

Zimmermann 2002, see discussion in the ecological comparison). The effects of this pattern on the sexual system and pollination are discussed below.

Gender and pollination

Protandrous trees were the majority in the study of Semm (1966, 2:1) and were equal in number to protogynous trees in Wittrock (1886), both studies compiled 100 trees or more. Haas (1933) and Vogler (1906) report a majority of protandrous trees (2-3:1) and de Jong (1976) and the current study a majority of protogynous trees (ca. 2:1), all of the latter however compiled less than 20 trees. Heterodichogamy splits the population into two reciprocally pollinated groups (Stout 1938, Cruden 1988) as manifested by the synchrony of the trees in the stand.

The flowering pattern at the tree scale may cause a vertical differentiation of character, making the crown bottom more protandrous (more male flowers in the first phase) and the crown top more protogynous (more male flowers in the second phase figure 18), or even (referring to fruit number, results before figure 20) making crown bottom more male and crown top more female. In addition, small trees may function as predominantly male as they set very few fruit, but have the potential to contribute pollen to many fruit of a neighbour with a reciprocal gender sequence. However, the findings are too limited to allow a full discussion of these possibilities. A possible vertical splitting of gender functionality within the crown, in addition to the heterodichogamous splitting of the sexual system (see discussion of *A. pseudoplatanus*) may be an intriguing theme for further study.

The low frequency of *A. platanoides* in the stand, which is typical for the species in Europe (Haas 1933, Roloff and Pietzarka 1998), together with heterodichogamy, may restrict pollination opportunities, as exemplified by the two neighbouring large trees which, being protogynous, cannot pollinate each other (figure 20 and see below). Still, seed per fruit rate is higher than in the more frequent and likewise heterodichogamous *A. pseudoplatanus*, suggesting a different pollination mode. The large distances between the trees make wind, thrips or nitidulid pollination rather improbable (the latter return to the same tree after agitation, looking for shelter). *Andrena* bees visit the flowers longer than *Bombus* bees, but both were observed on the flowers in an abundance that seemed high enough to enable the pollination of a large proportion of the flowers (if these bees are indeed effective in

pollinating the individual flowers they visit). The curving of stamens inwards during flowering (plate 6, also observed by Wittrock 1886) may be effective in contacting the bees in a similar location to that with which they touch the stigma, and may also be seen as a form of pollen portioning (Yeo 1993, Leins 2000).

Effective transfer of pollen between trees can happen only if the bees frequently change the tree they are feeding on, because of the temporal dioecy caused by heterodichogamy (Cruden 1988). The trees are far apart and each offers the bees plenty of food (Arroyo 1976), so why should bees frequently change trees? Suggested explanations are different quantities, nutrient constitution or toxic components of nectar among trees (Pleasants and Zimmermann 1979, Rhoades and Bergdahl 1981, Frankie and Haber 1983, Adler 2001, Herrera et al. 2006), discouragement by declining resources (Stephenson 1982, Bell 1986, Ito and Kikuzawa 2003) and behaviour mechanisms in the bees (Kevan 1990, Chittka et al. 1997), but these were not studied. Differences in nectar quantity were reported by Haragsim (1977) in *A. pseudoplatanus* and not in *A. platanoides*, but these still may exist. Maybe the observed difference in the color of the disc between male and female flowers plays a role in regulation of pollinator attraction.

Selfing is very limited by heterodichogamy. However due to the vertical pattern of flowering there is some overlap between male and female phases in the tree. It may be seen as enabling selfing or as disturbing outcrossing, and may make a difference in seed quality between top and bottom crown. Top to bottom selfing may occur at the beginning of female phase in protandrous trees and bottom to top selfing may occur at the end of the female phase in both gender sequences. Both abiotic and biotic vectors are thinkable for both processes – the former may be facilitated by falling pollen (compare to Meeuse et al. 1989), falling of small insects (observed) or foraging patterns of bees (Kevan 1990), the latter could be due to air turbulence (Nathan and Katul 2005), rising air masses, or a different insect behaviour, but seems less likely. Fruit set was higher at the top than at the bottom of the studied tree, fitting the findings of Acatay (1938) and Semm (1966, older trees) that also showed that seed from upper crown were usually more vital. Fruit number per infructescence in this study is much higher than reported by Acatay (1938) and somewhat higher than in Semm (1966) probably due to the larger tree size.

Acer pseudoplatanus

Heterodichogamy is a rare and poorly understood sexual system (Renner 2001, Barrett 2002). As a special case of temporal dioecy (Cruden 1988), it splits the sexual system into two reciprocal groups. Heterodichogamy is regarded as the temporal equivalent to heterostyly and is likewise suggested as a pathway to dioecy. This section attempts to through some light on heterodichogamy in *A. pseudoplatanus*, its relation to the pollination mode and suggests a generalisation that underlines the ecological role of the temporal separation of gender.

The heterodichogamous sexual system

Heterodichogamy in the monoecious *A. pseudoplatanus* and the quite strict synchrony of its flowering phenology (figure 24, table 12) split the population into two groups of trees. Protogynous trees, the first to flower female, took a smaller proportion in the stand (1:3) and had less female flowers per inflorescence (1:3-4) than protandrous trees (figure 22, plate 5). The stigmas on protogynous trees received more pollen per stigma (figure 25b, ca. x15, depending on the measure used), the inflorescences had more adult thrips during the female flowering phase (figure 26, x2-3) and the trees had more seeds per fruit (x3-4) and more seed per tree (x3) than protandrous trees (figure 27, tables 15 and 16). Protogynous trees as a group produced the same number of seeds as protandrous trees as a group (table 16, plate 5).

Former studies of *A. pseudoplatanus* were usually done in less mature or less natural stands (roadside and arboretum trees in de Jong 1974, small isolated populations in Binggeli 1992, however Semm 1966 studied a mature mountain population). The use of the crane in this study enabled the inspection of whole canopies of many mature trees in a semi-natural stand (table 1, figures 42 in the appendix, and plate 1). The treatment of whole crowns was accompanied by a methodological approach of typifying individual trees by their largest inflorescences and concentrating on the phenological data, which is different from e.g. de Jong (1976), who documented the variability of inflorescences within the trees.

The asymmetry in tree number here is relatively large compared with 7:5 (protandrous to protogynous, de Jong 1976, medium trees 3:1, larger trees 4:3) and 1:1 in Semm (1966) and Binggeli (1992, variability among small populations ranging 3:1 to 1:4). Male trees are rare here, as in de Jong (1976), Binggeli (1992) and Semm (1966 – data of 1963) but different

from Semm (1966 – data of 1964, 20%) and Scholtz (1960, 44%). The latter author, however, reports several unintelligible facts such as many hermaphrodite flowers, and thus probably used a different methodology and is left out in the following (see also Svobodová 1973). The differences in flower number between the types were reported by Semm (1966) and Weiser (1973), and some differences in infructescence structure were observed by Binggeli (1992). A detailed phenological study and the analysis of pollen on the stigmas, thrips in the inflorescences and seeds per fruit were as far as I know not done before.

The gradual curve of functional femaleness is similar to Binggeli (1992) and Semm (1966). However in the former protogynous trees are more female (other than here, figure 23) and in both the male to female flower ratio is higher than here (ca. 6:1 versus 2.5:1). The countings are not directly comparable as they refer to different inflorescences (here the largest inflorescences were taken, in Semm 1966 and Binggeli 1992 the average inflorescence size is about 2/3 as here) and use different methods (here categories, there exact counting).

The protandrous trees seem to increase in their femaleness measure with increasing height above 25m (figure 23b), which suggests a gender specialisation with tree size (Bawa and Lloyd 1984). The absence of small protogynous trees is somewhat surprising, and contrasts their being a half of the small trees in de Jong (1976). Changes of gender sequence were found neither here nor in Binggeli (1992) and de Jong (1994; 1976 reports some changes in few inflorescence only per tree). Other *Acer* spp. were found to change gender to some extent in respect to tree size and growth habitat, but these were usually more or less dioecious species (Hibbs and Fischer 1979, Sakai and Oden 1983, Primack and McCall 1986, Sakai 1990, Matsui 1995, Ushimaru and Matsui 2001, Nanami et al. 2004).

The synchrony of flowering is on inflorescence, tree and stand levels (figure 24, tables 12 and 13). It is exemplified by the constancy of flowering duration between 2004 and 2005, although both flowering intensity and herbivore damage were very different, by the strong synchrony of reciprocal gender phases between the groups (table 12) and by the correlation of starting and ending dates of female flowering (table 10). The pauses between stages are an important factor in this regulation. The clearest pause is between first male stage and the female stage of protandrous trees (table 11, figure 24, similar to Svobodová 1973, and Vogler 1906 in *A. platanoides*), which is the pause that has the greatest potential of disturbing the synchrony, as it is the only male to female transition. The different measures of synchrony are

qualitatively similar (table 12 and see discussion for *F. excelsior*). De Jong (1976) reports protandrous trees to start flowering two days earlier than protogynous trees and also a flowering time constancy of individual trees, which were not observed in this study.

Grube (1988, see also Leins 2000) studied the flowering phenology of three trees, and reached the conclusion that it was correlated with the climate, especially that the second male phase began after a minimum of temperature. In this study the flowering of the first gender was during a warm period and ended with rain, but no further relation was found. Norby et al. 2003 warmed branches of other *Acer* spp. in 4°C above the environment for the whole year, and obtained an earlier flowering in one week (when winter was cold enough) which is actually a small effect in relation to the scope of intervention. As weather at the flowering period does not supply clear cues but the trees are highly synchronised, it is probably a different factor that is responsible for it, maybe day-length (Lehrbuch der Botanik für Hochschulen 2002).

The basic pattern of flowering in the inflorescence is described by de Jong (1976 and 1994, based on Wittrock 1886) as a strictly alternating expression of male and female gender, and flowering sequences of individual trees are interpreted as parts of this basic pattern (figure 37, left). An alternative basic pattern is suggested to be gender determination in each one of the consequent flowering phases separately (figure 37, right, based on Haas 1933 for *A. platanoides*). This pattern fits better the findings of multiple consequent male phases (in the male tree and in a half of the protogynous trees, figure 24, plate 5, and similar observations by Grube 1988, and Bendixen 2001 for *A. campestre*) and the numeral and structural differences between the female phases of protandrous and protogynous trees. The suggested pattern also fits better the experimental findings of de Jong himself (1976, e.g. changes of sexual expression of the remaining flowers after cutting flowers that would have been female) and his observation (and also Haas 1933, Grube 1988 and here) that the gender of a flower is determined shortly before its anthesis, explaining the non-dehiscing anthers in female flowers and pistil rests in male flowers, especially in the second male phase.

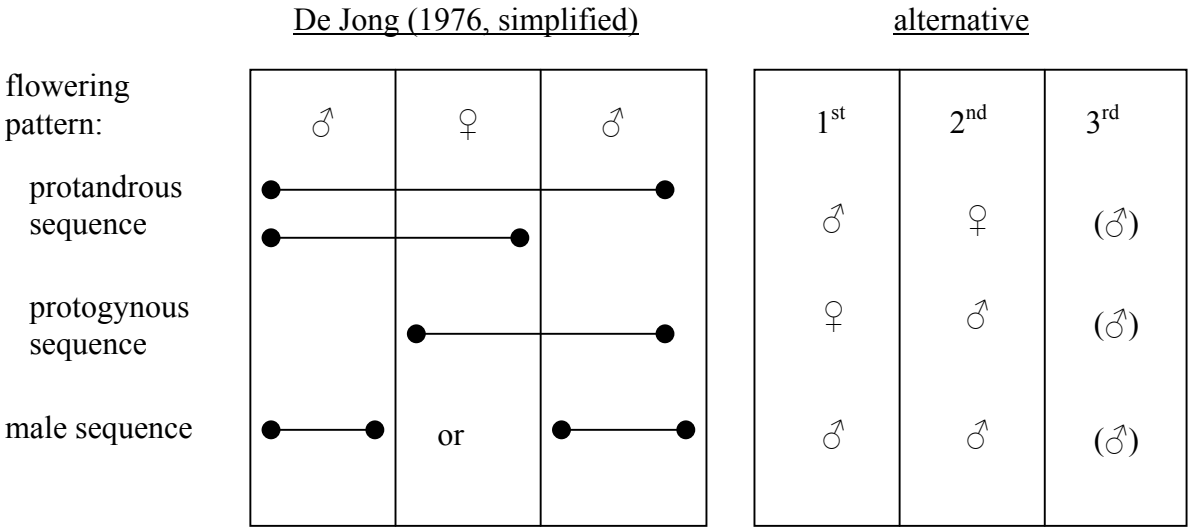

Figure 1: Schematic representation for the commonest gender cycles in *A. pseusoplatanus*. Left after de Jong (1976 and 1994) and right suggested here. Flowering phases are separated by lines, ♂ and ♀ represent male and female flower groups respectively, (♂) denotes male flowers that are found as a third phase in the largest inflorescences, commonly having large pistil residues and occasionally including female flowers.

The number of carpels per flower was shown to be variable (figure 27, as reported already by Buchenau 1861 and Pax 1885), but not connected to the gender sequence (other than in Binggeli 1992). The number of carpels was tree typical (results after figure 27) and as such might be inherited and considered as a means to increase seed number per fruit. Stigma length is generally much larger than in the figures of de Jong (1976). The gradual lengthening of the stigmatic lobes may enhance pollen tube competition, as grains landing on the edge of the lobe at the beginning of anthesis may compete with grains arriving later but landing on an inner part of the lobe. Indeed significantly more pollen grains were found on the outer part of the stigma than on its inner parts (results after table 14). Stigmas of protogynous trees seemed longer and thicker than stigmas of most protandrous trees, which may indicate a potential adaptation to a different pollination agent (see below) but these differences were not quantified. Variability in pollen size was not found between protogynous and protandrous trees as groups, but individual trees as well as regions within the crowns differed significantly, indicating that a larger sampling is needed to understand the pattern of variability of this parameter.

Male flowers suffered larger florivore damage in 2005, irrespective of the gender sequence of the trees (results after figure 23). For foliage herbivory, Binggeli (1992) proposes that protogynous trees suffer more herbivory (cited in Leather 2000) and in dioecious *A. negundo* males suffer more herbivory (Jing and Coley 1990). These observations are according to the commonly observed male biased herbivory (Årgen et al. 1999, Ashman 2002, Verdú, Gracia-Fayos and Gleiser 2004, Cornelissen and Stiling 2005).

The length of fruit wing and the angle between wings were variable in similar ranges within and among trees as reported by Vogler (1907), but were found to be larger in the year of full flowering and high pollination level (2004) than in the year of partial flowering and lower pollination level (2005), thus not tree specific and possibly indicating fruit vigour. The differences in wing form strongly affect the fruit's aerodynamic features (Sipe 1995) and thus its dispersion ability. Semm (1966) found that fruit and seeds of protandrous trees are lighter than those of protogynous trees (the comparison here is of too few trees, table 18).

The difference in seed set between protogynous and protandrous trees is referred to only by Binggeli (1992, Semm 1966 found such differences in *A. platanoides* and *A. campestre* but not in *A. pseudoplatanus*), suggesting to use it together with different structural details of the infructescence to distinguish gender sequence after flowering. This suggestion is supported by the analysis of fruit and seeds in the largest infructescences (table 15) but seems to be caused by different pollination levels (results after table 17) that may be different in other regions. Methodological, the use of the largest infructescence solved the statistical deficiency of comparing the protandrous and protogynous groups using the medians (or averages in other cases) for individual trees and ignoring the variation within each tree. The inner variability would have probably weakened the significance of the findings, but as the differences were large, probably would not have changed the results themselves. The comparison of the largest infructescences may enable a convenient determination of tree sequence type, supporting Binggeli (1992).

The large number of empty fruit (figure 27) is surprising, as it seems to take many resources from the trees producing them (Ho 1992). The production of an empty mericarp when the other mericarp is full may be explained by the development pattern of the fruit as a whole, but why do some trees produce every year up to 95% fruit with two empty mericarps? A possible explanation is that the green winged fruit may be self-supplying assimilates for its growth and

the tree supplies the nutrients for the seed only. The proportion of the weight of the wing from a full mericarp (table 18) was found to be similar to the results of the physiological study of Bazzaz et al. 1979 (for *A. platanoides* and winged fruit of other temperate trees) and Cipollini and Levey 1991 (with radiation level from Stoutjesdijk and Barkman 1992). To judge on the increasing weight of the wing in the sequence two empty mericarps, empty mericarp with the other mericarp full and full mericarp (table 18), the tree and the fruit wing seem to split the production cost of the fruit wing (maternal tissue) at a 1:1 ratio. The production of many empty mericarps may be also connected to the late development of the embryo (Hong and Ellis 1990), possibly a strategy of choosing among embryos (Stephenson 1981, Ho 1992).

Selfing is reported to be important by Semm (1966, claims it is a major factor) and Pandey (2005, median 10%). In this stand the high seed set of protogynous trees and the long pause between male and female phases of protandrous tree (table 11, figure 24), render selfing improbable as a major reproductive factor for most of the tree crown, but it may play a role in lower parts that change gender before crown top (table 13). Selfing rates and their dependency on the population structure were studied by Pandey (2005), but he did not relate them to gender sequence types, the flowering phenology nor to the pollen vector.

Thrips pollination

The most important difference between the types is the difference in seed set – protogynous trees produce many more seeds per tree than protandrous trees (table 15, figure 27). As this difference is strongly correlated with pollination level (figure 25b), and the pollination level is strongly correlated with the number of adult thrips in the inflorescences at female flowering time (figure 26b), it may be that thrips are the main pollinators.

Thrips are renown for their abundance in flowers (e.g. Darwin 1876, 1877) and may especially well act as pollinators of large trees, as they may quickly become abundant ("Thrips appear to be ideal animal pollinators for mast-fruiting species" Ashton et al. 1988).
There are several reasons to consider thrips as pollinators of *A. pseudoplatanus* in the study area:

1. Their abundance (figure 26a, Grube 1988), capability to transfer pollen (personal observation, Proctor et al. 1996), flight ability (Kirk 1996 and 1997) and association

with the flowers as their reproductive site (Teulon et al. 1998, Sakai 2002, Dufaÿ and Anstett 2003).

2. The correlation of the number of adult thrips in the inflorescences with the pollination level in these inflorescences (figure 26b).
3. *A. pseudoplatanus* has several characters adequate to thrips pollination (Kirk 1997) such as compact inflorescences (de Jong 1976), many flowers per inflorescence, much pollen per anther (Grube 1988), and a quite powdery pollen (Hesse 1979).
4. Bees and flies, to which pollination was accredited (Müller 1879, Knuth 1898, Grube 1988, Binggeli 1992, Proctor et al. 1996) were much too rarely observed to account for pollination of so many flowers.
5. Wind pollination was held responsible for a part of the effective pollination by Semm (1966) and Binggeli (1992) and may play a role as pollen is easily blown away (Hesse 1978) and is found within tree crown and in the air (Rempe 1938, Hyde 1950, Andersen 1974a). However it is impeded by foliage and may only partially explain the difference between the gender sequences (see below). Wind pollination was inferred by exclusion of insects with nets of 1mm mesh size (Binggeli 1992) which do not exclude thrips.

The evidence for thrips pollination in *A. pseudoplatanus*, however, is only circumstantial, as exclusion experiments (similar to those of Moog et al. 2002) failed because of technical difficulties. As a side remark, the biology of *Taeniothrips inconsequens* on *A. pseudoplatanus* may be commercially interesting from the entomological aspect, as it is a pest of sugar maples in North America (Childers 1997, Parker and Skinner 1997), and *Ceranisus pacuvius*, the parasitoid wasp that was found in the inflorescences and within thrips assemblages, may be a parasitoid of it (Teulon et al. 1998, Loomans 2003, Cameron et al. 2004).

If thrips are the main pollinators, their function as brood-site pollinators (Sakai 2002, Dufaÿ and Anstett 2003) is probably responsible for a higher seed set in protogynous trees, having their female flowering at the time when adult thrips are more mobile. As the thrips emerge earlier than the flowering time of *A. pseudoplatanus* (they were already found on *F. excelsior* and *A. platanoides*), they may exert a selection pressure towards earlier flowering on protandrous trees (to be the first to donate pollen) and on protogynous trees (to be chosen as a breeding site).

Patterns of germinating pollen grains on the stigma is interpreted to imply which pollination agent deposited them. Pollen group sizes were small (results after table 14), but double in frequency and size than Rempe's (1938) results for *A. pseudoplatanus* pollen the crown space. The rarity of larger groups of pollen (which may be attributed to larger pollinators such as bees) may imply that these did not play a significant role in pollination and the greater size and frequency may imply some concentration of the pollen by a small pollinator. However, this (novel) suggestion must be experimentally tested in controlled pollination experiments. Wind pollination may well play a role as pollen is found in the air, and may also partly explain the difference in pollination intensity between the types due to the numeral ratio of male to female flowers (3-4:1, see the next section). However the ratio in pollination intensity was much higher (ca. 15:1), possibly indicating a more efficient transport agent. In respect to Rempe's (1938) reported density of pollen in the air (7-17 grains/mm^2), the pollen density on the stigmas is low (ca. 2 grains/mm^2), maybe due to the strict dichogamy (a female phase tree can receive pollen only from neighbouring trees). Both wind and thrips pollination probably facilitate close range pollination, which may depend on a high tree density and bring about small breeding communities (Thompson 1999, Pandey 2005).

The floral characteristics of *A. pseudoplatanus* are much closer to the anemophilous syndrome than a generalised entomophily would imply. If thrips also exerts a selection pressure towards earlier flowering, the main difference to the anemophilous *F. excelsior* is the location of the inflorescence – lateral inflorescences enable flowering before leaves unfold (Ogata 1967). The change from terminal to lateral inflorescences is a main distinguishing feature between entomophilous and anemophilous species of both *Fraxinus* and *Acer* (Wallander 2001, Ogata 1967, respectively), and is connected to more elaborate changes in vegetative traits such as growth form and leaf size (Sakai 1990, Verdú and Gleiser 2006). This suggestion is a principally different kind of transition from entomophily to anemophily than the one proposed by ambophily (Culley et al. 2002), as the intermediate state is in a sense specialised, and not just a mixture of the original and final states.

Heterodichogamy: Asymmetries and reproduction

The heterodichogamous sexual system of *A. pseudoplatanus* is characterised by asymmetries between protandrous and protogynous trees in many aspects of their reproductive biology: Tree number (figure 22), number of female flowers per inflorescence and thus functional gender (figure 23a), period of female flowering (figure 24), pollination efficiency (figure

25b), thrips in the inflorescences (figure 26) and fruit and seed set (tables 15 and 16, figure 27). The following is an attempt to model the interaction of these factors with the aim to understand the influence of numeral ratios and pollination effectivity on the resulting reproduction.

I first assume all trees are identical in size and in their breeding opportunities (i.e. random mating, fully synchronized flowering phenology between reciprocal gender phases, simultaneous flowering of all flowers in a gender phase). The parameters left are the numeral ratio of the trees (**A** protandrous to **a** protogynous trees in the stand), flower number per inflorescence (**F** female flowers in protandrous to **f** female flowers in protogynous trees, **M** male flowers assumed equal in both and only two gender phases are assumed) and an abstract pollinator efficiency that may be different in the two phases ($\mathbf{p_1}$ and $\mathbf{p_2}$ respectively), as presented in figure 38. In addition to pollinator efficiency, the sheer numeral ratio of male to female flowers at flowering time may affect the success of pollination. This ratio is presented to the right in figure 38, and assumed to differ between the phases in linear dependence on the ratios of tree and flower numbers.

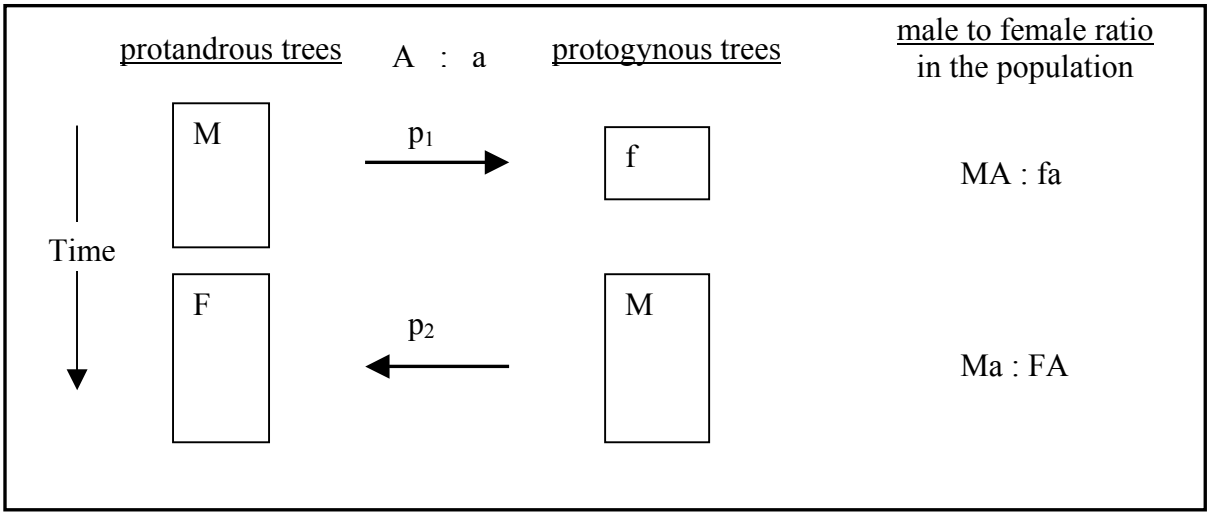

Figure 38: A scheme for the simple model of the role of the asymmetries in the pollination of the heterodichogamous *A. pseudoplatanus*. The rectangles represent the two reciprocal gender phases in both types, in which **M** is the number of flowers per inflorescence in the male phase and **F** and **f** are the numbers of flowers per inflorescence in the female phases. **A** and **a** are the numbers of trees of each gender sequence in the population, $\mathbf{p_1}$ and $\mathbf{p_2}$ are the pollinator efficiencies in the two phases.

The relative success of reproduction is calculated per individual tree under two assumptions in the following way (summarised in table 24):

1. Tree and flower proportions only (full pollination) - Female success is equal to the number of female flowers, male success is equal to the number of female flowers of the reciprocal type divided by the ratio of male to female trees to express the equal distribution of siring success among all trees in the same phase (analogous to Lloyd's 1980 equivalence parameter E).
2. Including pollination efficiency – The success calculated above multiplied by two factors – the overall ratio of male to female flowers (determining pollen potentially available per stigma) and pollinator efficiency.

Table 24: Success of individual trees (protandrous and protogynous, at male and female phases) under different assumptions regarding the factors that influence pollination (see text).

gender phase	success per tree (tree and flower proportions only)		including pollination efficiency			
			factors (figure 38)		success per tree	
	protandrous	protogynous	overall male to female ratio	pollinator efficiency	protandrous	protogynous
1st	f·a/A (♂)	f (♀)	M/f · A/a	p_1	M·p_1 (♂)	M·p_1· A/a (♀)
2nd	F (♀)	F·A/a (♂)	M/F · a/A	p_2	M·p_2· a/A (♀)	M·p_2 (♂)

The ratios of success of individual trees (protandrous to protogynous) in their female and male function may indicate the resulting relative maleness and femaleness of the two types (table 25) . I use the approximate values from the results in 2004 to substitute the parameters – A/a=3 (figure 22), F/f=3 (figure 22), p_1/p_2=3 (figure 26, assuming thrips pollination and taken as the ratio of adult thrips in the first and second phases of flowering) or p_1/p_2=15 (after number of pollen on the stigmas, figure 25b).

Table 25: Ratio of female and male success of protandrous to protogynous trees under three assumptions. The values approximate the relations in the study.

assumption		ratio of success of protandrous to protogynous individual trees (from table 24)			
		female function		male function	
tree and flower proportions only		F/f	3	$f/F \cdot (a/A)^2$	1/27
pollination efficiency as male to female ratio only		$(a/A)^2$	1/9	1	1
full pollination efficiency (including pollinator) *	3: 15:	$p_2/p_1 \cdot (a/A)^2$ (pollen on stigma)	1/27 1/5	p_1/p_2 (pollen on stigma)	3 15
* The values 3 and 15 are for p_1/p_2, after thrips abundance and pollen on stigma, respectively.					

It turns out that the relative gender of the two types strongly depends on the assumptions regarding pollination efficiency (table 25). The model indicates the following conclusions:

1. Ignoring pollination efficiency, or if pollination efficiency is equal for all trees, protandrous tree may be regarded female and protogynous tree may be regarded male (reflecting flower number in female stage, somewhat similar to the calculation of functional femaleness in figure 23a).
2. Taking into account both factors of pollination efficiency – total male to female ratio and pollinator efficiency both higher at the first phase, the opposite relation results. This situation may be seen as represented in this study – the protogynous trees have a greater contribution in the female gender, the protandrous trees have a greater contribution in the male gender.
3. In these two conclusions, a 1:1 ratio in the population leaves the situation qualitatively unaltered (!). Only a higher frequency of protogynous trees may cause a situation of equal male and female fitness of the two types. Under the first assumption because of flower number asymmetry, in the last assumption due to different pollinator efficiency.
4. Ignoring only the pollinator efficiency, which is similar to regarding habitats where pollinators are abundant, and their efficiency is not related to the number flowers, protogynous trees are superior to protandrous trees in female gender and equal in male

gender as long as they are in minority. I.e. – an equal number of trees from the two types is expected.

The calculation demonstrates the dependency of the relative success of the two types as male and as female upon the pollination efficiency and numeral ratio of the trees in the stand. It thereby underlines the splitting of the sexual system as a kind of a natural experiment in pollination efficiency, enabling the species to rely on two different types of pollinators. When pollinators are abundant throughout the season (e.g. bees, other feeding only insects, and also wind, is effective) protandrous trees could produce many fruit due to their larger flower number, but when these pollinators fail, the protogynous tree may still be pollinated by the brood-site pollinator thrips. It is thus interesting to compare the seed to fruit ratio of protandrous and protogynous *A. pseudoplatanus* at a part of its geographical range where bees are abundant at flowering time.

Heterodichogamy as a pathway to dioecy? In the studied stand in the studied years and judging upon flower number protogynous trees are relatively male and most protandrous trees are relatively female (figure 23a). Without regarding the numeral asymmetry and the pollination efficiency, this seems to support the consideration of heterodichogamy as being on the pathway to dioecy (Ogata 1967, Ross 1982, de Jong 1994, Renner 2001, Verdú and Gleiser 2006). Other heterodichogamous species have a ±1:1 ratio between plants of protandrous and protogynous gender sequences e.g. tree species of Juglandaceae (Gleeson 1982, McCarthy and Quinn 1990, Kimura et al. 2003), *Thymelaea hirsuta* (Dommée et al. 1990 and 1995, Ramadan et al. 1994, El-Kebawy et al. 1996, ratios depending on environment, protandrous plants were more female, interestingly thrips pollination was newly reported for this species by Cornara et al. 2005) and *Grayia brandegei* (Pendleton et al. 1988 and 2000 – 1:1 ratio, protogynous plants were more female) and heterodichogamy in these species was interpreted likewise, mainly due to the finding that the sexual type that was functionally more female also produced most seeds.

In the current study, however, the "male type" protogynous trees had more seeds (tables 15 and 16, figure 27) than the "female type" protandrous trees. The model presented above suggests that heterodichogamy functions in *A. pseudoplatanus* to enable utilisation of different "pollination ecotypes" (Fenster et al. 2004 and references therein) found in the range of the species. The maternal success of protandrous type seems to depend upon an efficient

and extensive insect pollination whereas the maternal success of protogynous trees is accentuated under brood-site pollinators or wind pollination regimes (the male success of the types show the opposite dependency). The suggested adaptations are at flower level (stigma morphology, number of carpels), inflorescence level (female flower number) and phenological pattern, as protogyny is connected with wind or beetle pollination whereas protandry with bee pollination (Willemstein 1987, Sargent and Otto 2004). The "pathway to dioecy", may perhaps open in cases when one of the strategies is consistently much better than the other, and the latter degenerates as a gender phase (or changes to the former, see figure 37).

Tilia cordata

Male flowers and gall midges

Tilia cordata is andromonoecious, and not hermaphrodite as described by former researchers (Eisenhut 1957, Corbet et al. 1979, Pigott 1991, Fromm 2003). In this study purely male flowers were found as a large minority of the flowers, and beside them, flowers with damaged pistils and gall flowers, both functionally male, were reported (figure 28, table 19). Cryptic andromonoecy was described in the close relative *Tilia japonica* (Ito and Kikuzawa 1999, Ito 2002), where seemingly hermaphrodite flowers with non-functional pistils were found. This may be also the case for the hermaphrodite flowers with thin and short style found in this study (figure 28, plate 7) and may relate to the occasional female sterility reported by Eisenhut (1957) and Klein (1992) in relation to seed production. Andromonoecy may thus be a wider spread characteristic of the genus *Tilia*.

Andromonoecy is interpreted as an enhancement of male fitness, partly dependant of environmental conditions and developmental plasticity (Primack and Lloyd 1980, Stephenson 1981, Bertin 1982, Miller and Diggle 2003, Cuevas and Polito 2004). The frequency of male flowers was highest at the beginning of flowering, and decreased as the total anthesis in the tree increased (figure 29). This tendency enhances the protandry of the individual flowers and causes a pattern of accentuated maleness at the beginning of anthesis and stronger femaleness at the end (figure 31c). This pattern fits to the theoretical model for the temporal pattern of resource allocation to male and female gender of Brunet and Charlesworth (1995) and may be also understood by the findings of Stephenson (1982) that in mass flowering trees the beginning of flowering mainly functions to attract pollinators while most outcrossing happens towards the end of flowering. However it is opposed to the tendency of many species to produce male flowers at the end of flowering (Avi Shmida, personal communication, Primack and Lloyd 1980, *Acer pseudoplatanus*, this study and de Jong 1976) and may relate to a possible relation of the male flowers to the gall midges (see below).

A new type of galls is described (figure 28, plate 7). Flower galls were not known in *T. cordata* in spite of the fact that many inflorescence galls were described (Ross and Hedicke 1927, Buhr 1964, Postner 1982). The galls are caused by gall midges (Cecidomyiidae) that oviposite into buds just before they start to swell and open. The gall flowers are not so much

deformed as they are damaged and arrested in development. The main deformation is the strong curving of the style due to the sticking of the stigma to other flower parts, which is probably caused by flower-own mucilage (Schumann 1890, Engler 1909) secreted in response to oviposition and larval activity (Dawn Frame, personal communication).

The species of the gall midges could not be surely determined, because only females were collected (during oviposition into the buds). However the three species to which the females may fit are either leaf gallers (*Dasineura tiliae* and *D. thomasiana*, described in Kieffer 1888 and Rübsaamen 1889, respectively) or inquilines (*Macrolabis floricola*, Netta Dorchin, personal communication). Thus it may also be a non-described species that causes this non-described gall form. The chalcidoid wasp *Omphale theana* may be a parasitoid of this gall midge species (its host is currently unknown, Stefan Vidal, personal communication). As the parasitoid was frequently observed, infestation rate may be high. The morphologically peculiar platygastrid wasp *Inostemma* sp. may be another parasitoid of the gall midges (Gauld and Bolton 1988).

The first and the last tree to flower had the highest frequencies of gall flowers, and it was neither correlated with the frequency of other male flowers nor with the stage of anthesis on the tree (figure 29). As buds were available several weeks before flowering and as gall midges were observe in a high density on buds when most buds were already flowers, this infestation pattern may indicate that successful oviposition is limited to a definite stage in bud development. The frequency of flowers with a damaged pistil increased at the beginning of flowering on individual trees and then decreased toward its end (figure 29). It was on the one hand correlated with the frequency of male flowers, and on the other hand pistil damage was similar to gall midge damage to the rudimentary pistil in gall flowers. Maybe these flowers developed from buds that were infested, but for some reason did not complete their forming to a gall flower (due e.g. to death of larvae, attack of parasitoids, oviposition in an inappropriate bud or increased vigour of flowers at specific location in the inflorescence, on the branch or on the tree). The connection between maleness and gall midges is not clear and needs a closer investigation on the ontogeny of male flowers and infestation dynamics (and see Price et al. 1980).

The trees in the stand present a large variation in flower number per inflorescence (figure 30a). This variation is larger than found by Eisenhut (1957), and even exceeds by far the

variation Eisenhut (1957) reported for the whole genus. Trees seem to be consistent in flower number per inflorescence in the short term at its extremes (figure 30b), but the small number of trees flowering in 2005 limited the comparison. Smaller canopy trees were found to have more flowers per inflorescence than large trees as a significant trend, with one conspicuous exception (figure 30b). This corresponds to an overall architectural change in mature canopy trees of reported by Eisenhut (1957) and may relate to changes in tree vitality as described by Roloff (2001). Within the sun crown differences were observed (figure 31b and adjacent results), but no consistent pattern was found, other than in Eisenhut (1957). The shade crown holds very few inflorescences (table 20, Eisenhut 1957).

Pollen grains are quite uniform in size, that is similar to Eisenhut (1957), but a significant difference was found separating the trees into two groups. As only eight trees were studied, and the difference was in magnitude of the measurement inaccuracy, further study must be undertaken before this difference may be interpreted. Within-tree differences and differences between pollen of male and hermaphrodite flowers were not conclusive (table 21).

Phenology

The intensity of flowering differed markedly between 2004 and 2005 (figure 5). Whereas in 2004 all trees flowered fully, in 2005 only large trees flowered (figure 31a). Such differences cause large differences in resources for insects that depend on the flowers. The local fluctuation was stronger in the southern part of the plot and milder in its northern part as the large trees were concentrated in the latter.

The most conspicuous phenological pattern within the individual trees was that the terminal inflorescence along a twig flowered last (plate 7). Other patterns were slight at best - a vertical pattern was overcast by local differences between branch groups, and south-north difference was evident only at the very beginning of flowering (figure 31b).

Male and female gender strongly overlapped at inflorescence and tree levels (figure 31c), thus overcoming the protandry of the single flowers and potentially enabling a very effective geitonogamy, as found to be common by Fromm (2001). Due to the protandry, at the end of flowering the dominating gender is female, thus outcrossing is more probable at the end of flowering, as reported by Stephenson (1982) for *Catalpa speciosa*. As the flowers in an

inflorescence open in a rather strict manner (Eisenhut 1957, Pigott 1991), more flowers per inflorescence imply a longer overall flowering and a higher overlap of gender. Interestingly, pollen was found to be deposited, to germinate and to develop pollen tubes on stigmas with unspread lobes, and even before the dehiscence of the anthers (!, but then only germinating pollen, with almost no pollen tubes, table 22, and similar to Anderson 1976 for *T. americana*). This counters the observed (morphological) protandry (Hildebrand 1869, Eisenhut 1957, Pigott 1991) as a functional character of floral phenology.

Pollination and insects in the inflorescences

The pollination mode of *T. cordata* is left unclear. Two major methodological limitations to its analysis were the limited observation time, especially the exclusion of night observation (moths may be main pollinators as found by Anderson 1976 and indicated by floral color and nectar production patterns, Eisenhut 1957, Corbet et al. 1979) and the failure of exclusion experiments due to herbivore and fungal damage to the covered twigs (and ant damage to the covers) and due to the difficulty to exclude thrips and still enable wind pollination. Wind pollination in *Tilia cordata* was suggested by Eisenhut (1957) as a main pollination mode, but was found to be of low importance by Anderson (1976) and Fromm (2001). The "main pollinator" may also differ within the species range and between years (Anderson 1976 and discussion in *A. pseudoplatanus*).

The pollination rate found here was low (figure 32), but pollen tubes grew well (other than in Britian, Pigott and Huntley 1981, where summers were usually not warm enough to support the completion of pollen tube growth), resulting in a low (3:1) germinating pollen to pollen tube ratio. The pollination level was higher in the upper crown than in lower crown (figure 33). In the tree in which this is most evident this situation is despite the findings that crown top started flowering later than crown bottom and that a higher proportion of male to hermaphrodite flowers was found in the lower crown.

Pollination patterns in the tree could in principal inform about the pollination mode as both wind and bee pollination may have distinct patterns of pollen dispersal with the tree crown. The spread of pollen by wind depends on the complex aerodynamical patterns within the crown (Niklas 1985 and 1992) and could be imitated by dyed particles (Kearns and Inouye 1993). *Bombus* on *Tilia* were found by Kevan (1990) to have characteristic movement

patterns in the crown as a whole that imply e.g. that more outcrossing is expected at crown top than at crown bottom (this may however also be an expected pattern of wind pollination due to gravitation, Meeuse et al. 1989, even if not as the syndrome they describe). A more elaborate sample is needed to confirm it as a general pattern, and the level of selfing could be studied using genetic markers such as in Fromm (2001). A comparison of the pollination patterns with *A. platanoides* may be worthwhile, as effects of dichogamy in relation to geitonogamy, of different potential pollinators (eusocial versus solitary bees) and of different aerodynamical conditions (existence versus absence of leaves) come into play. It may be interesting to study the reasons for tree changes by bees (Bell 1986, Kevan 1990, Ito and Kikuzawa 2003) and their relation to the production of male flowers.

In respect to stigmatic area, pollen density is about one tenth of the expected density after Rempe (1938, 12-68 pollen grains per mm^2). This however may result from different collecting methods (size, orientation of the collector and the duration of collection, as female anthesis is later than male anthesis). About a half of the pollen is deposited in small groups, remarkably similar in size and frequency to pollen groups found within tree crowns by Rempe (1938, 38.5% of the pollen in groups, average group size 4.09 grains), but smaller than pollen groups reported by Götz and Wolf (2004, 5-14 grains per group). The strong correlation between group number and total number of pollen suggests that grouping is not an artefact. Larger groups were found among the pollen tubes, suggesting a tunnelling of pollen tubes in the style and a possible intensification of the pollen tube attrition (Mulcahy and Mulcahy 1987, Németh 2005). The size and number of pollen groups on the stigmas may be seen as indirect evidence to the pollination mode, assuming that pollinators of different sizes and behaviour at the flowers may leave differing “pollen traces” on the stigma. This suggestion is, as far as I read, novel, and has to be check by observing “pollen traces” of insects in controlled pollinations, a study which is beyond the scope of the current one. If this suggestion holds, and bees are expected to deposit pollen in larger groups than the size of a clump falling from the anther, whereas wind (and thrips?) deposits groups in their original size, then about 80% of the pollination was done by wind (figure 32, proportion of group size below 10 from all pollen grains).

Insects were abundant in the inflorescences. Some were reproducing species (thrips, nitidulid beetles, gall midges, one species each) and others were a host of floral visiting insects, including predators and parasitoids of the reproducing species and several nectar feeding

chalcidoid wasps species. The interconnections among the species are presented in figure 39, based on observation and literature.

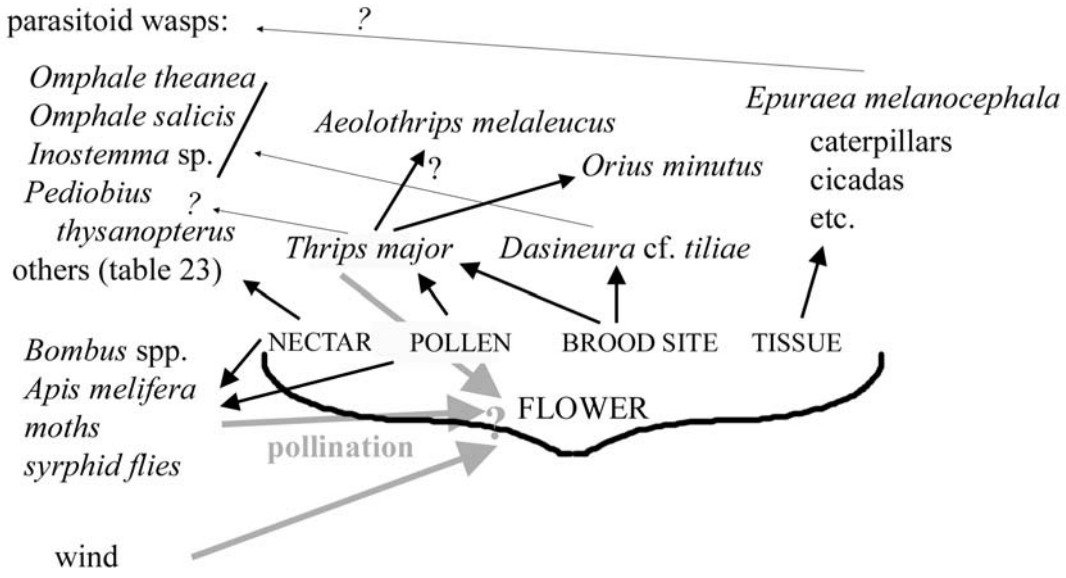

Figure 39: Interactions among the flowers of *Tilia cordata* and their insect visitors (observed and supposed). Thick grey arrows denote possible pollination (see discussion in the text), regular black arrows point from food to feeder or predator, the thin arrows point from hosts to parasitoids. Question marks denote possible relations (Mound et al. 1976, Gauld and Bolton 1988, Loomans et al. 1997, Sabelis and van Rijn 1997) that were not directly observed.

This net of interactions may be interesting from an entomological point of view, as the *Macroglenes* sp. (Pteromalidae) may be new to science and the genus *Ionympha* (Eulophidae) is not known from Germany (both Stefan Vidal, personal communication). Also, the host of *Omphale theana* (Eulophidae) is probably the gall midge species, and possibly *Pediobius metallicus* (Eulophidae) is a parasitoid of *Thrips tabaci*, which is a common pest (Loomans 2003, the cogener *Pediobius thysanopterus* Burks is known to parasite the genus *Gynaikothrips* - Loomans et al. 1997). The diagram also examplifies the potential complexity in changes of sexual system and pollination mode, as it was shown that gall midges may be relevant to the former and thrips may be relevant for the latter (see also discussion of thrips pollination in *Acer pseudoplatanus*).

Fruit

The total yield in the stand fluctuated between 2004 and 2005 (figures 6, 34 and 35) due to fluctuating flowering intensity (figures 5 and 31a). It is thus indicating a masting behaviour (Kelly and Sork 2002), although a longer observation period is needed to determine its regularity. As the flowering and fruiting trees in 2005 were the largest in the stand, it seems that this "masting behaviour" is related to the economy of scale (Herrera et al. 1998) or to nutritient availability (e.g. Sork et al. 1993, Miyazaki et al. 2002, possibly the extent of mycorrhiza, Newbery 2005) and not to climatic fluctuation or satiation of seed predators (Janzen 1971, Tapper 1992, Kon et al. 2005).

Most fruit is produced by a few trees (figures 6, 34 and 35), which are the largest in the stand (figure 34c). Thus these donate most prominently to the gene pool of the offspring, at least from the maternal side. As geitonogamy is frequent in *Tilia cordata* (Fromm 2001), probably in a pronounced extent on large trees (Arroyo 1976) and also as flower number increases with tree size, these few trees are probably also the main paternal donators. As tree size persists from year to year, and the large trees also flower more frequently (figure 31a), this effect may act in the long-term and have important consequences for the genetical structure of the population. This finding underlines the importance of the competition for space among canopy trees (Roloff 2001 and 2004, see also appendix).

The "flower to fruit ratio" here is only an approximation to the real flower to fruit ratio on the tree as it ignores the proportion of fruitless inflorescences, which may also differ among the trees. Whereas the common flower to fruit ratio in 2004 is 3-4, the regression shows that eight additional flowers are needed for one additional fruit, reflecting the error of the approximation (note that the constant of the regression is two and not zero). The variability among the trees may be either due to differing pollination efficiency or to differing frequencies of male flowers, but these were not studied here. A higher ratio in 2005 (4-6) may reflect the reduction in pollination due to a reduced flowering intensity as reflected by the percent of empty fruit. These ratios are similar to Anderson (1976, see also Sutherland and Delph 1984). Some trees have an exceptionally high flower to fruit ratio in 2004 (figure 34a) and this is probably not due to lacking pollination as they are neither spatially nor temporally isolated. It may reflect a higher male flower ratio, that was however not checked on these trees.

Most fruit contain one seed. Still several trees have over 20% of double seeded fruit, almost no empty fruit and many fruit per infructescence, which may indicate a more intensive pollination (Eisenhut 1957). On the other hand several trees have many empty fruit, and the overall proportion of empty fruit is higher in 2005, when flowering was of lesser intensity thus indicating lacking pollination. These grounds are different than those Pigott and Huntley (1981) found for British stands, in which a minimal warmth sum was prerequisite for a successful pollen tube growth and fertilization (2004 and 2005 resemble each other in their temperature sums, see appendix). The proportion of three seeded fruit is similar to Eisenhut (1957). In crown top fruit contain more seeds than in crown bottom, also fitting the corresponding data to pollen on the stigmas. Most trees seem self compatible (as in Fromm 2001), but as seed number was not checked, a conclusion cannot be reached. The much lower seed per fruit rate in 2005 in respect to 2004 (figure 35b) may indicate that geitonogamy is not so strong as Fromm (2001) suggests, because it was also found in the trees that flowered in full intensity in 2005.

An ecological comparison of the species

This last section of the discussion (1) draws a comparison of the reproductive biology between the studied species, and (2) returns to the "old question" of separation of gender and transition towards wind pollination in temperate forest trees, and checks what new insights were achieved by the "new means" - crown research using the canopy crane. It is organised after themes and relates to the main findings that are discussed in more length in the discussion of the species above.

Relation to environmental factors

Climate, leaf appearance and insect abundance are main factors effecting the phenology and reproduction of the studied trees:

1. Climatic effects are manifold. In the beginning of the flowering period temperatures play an important role, especially the timing of cold periods was found to shape the flowering phenology of *F. excelsior* (table 29 in the appendix). The decrease in the frequency of cold periods during March and April together with the increasing frequency of sunny periods (but also of strong rains) are the basic climatic gradient that may affect the trees flowering along it (appendix, Geiger et al. 1996). Temperature effects may reach well into the summer as shown by Pigott and Huntley (1981) – insufficient temperature sums may inhibit pollen tube growth and successful pollination as in *T. cordata*, but not in *A. pseudoplatanus*, in Britain (Pigott and Huntley 1981, Pigott and Warr 1989, Pigott 1992). The length of the vegetation period may limit successful reproduction in late flowering species as energy and assimilate supply needed for fruit ripening cease with leaf fall (Pigott 1981). Indirect evidence may be seen in the fact that seeds of *A. platanoides* are germinable before they are ripe (Hong and Ellis 1990).
2. Leaf appearance at the beginning of May has several implication to flowering phenology:
    a. Assimilate supply begins, affecting the whole physiological mode of the tree, including available resources to flowering and their allocation pattern (Tyree and Zimmermann 2002).

   b. Unfolding leaves attract herbivores, especially aphids, which may damage flowers that appear at the same time (Wellings and Dixon 1987).
   c. The green background reduces the showiness of the flowers as compared to bare trees (at least optically).
   d. The closing of the canopy creates a different microclimate in the forest, changing temperature and humidity gradients (figure 44a in the appendix, Stoutjesdijk and Barkman 1992, Geiger et al. 1995), as well as wind conditions (Wilmers and Ellenberg 1986, Nathan and Katul 2005). Leaves impede wind pollination severely (Whitehead 1969).
3. Insect abundance increases during early spring and spring to a peak in summer (e.g. Freeman 1945, Prŷs-Jones and Corbet 1987, Baal 1993). Not only insect numbers increase, but also their possibilities to be active (Corbet 1990). This must not have direct implication to specialised pollination systems, which may depend on a specific early spring insect (Schemske et al. 1978, e.g. solitary bees in Müller et al. 1997 or bumblebee queens, Motten 1986), but may be important for trees that, having a huge number of flowers to be pollinated, are probably relatively generalists (Heinrich 1975). Especially important insects in this respect are bumblebees, which are common pollinators (also for the studied trees – Müller 1873, Corbet at el. 1979, Kevan 1990), that come in large numbers due to their eusocial community structure (Prŷs-Jones and Corbet 1987). Their colonies increase in number, until a peak is reached in July with the flowering of *Tilia* spp. (Baal 1993).

The main interactions of the flowering and pollination of the tree species with ecological factors may be categorised as conflicts (problematic ecological factors to the reproductive biology), resolutions of conflicts (reproductive characters that overcome potential conflicts), and ecological factors promoting pollination. These interactions for the studied species are (figure 40):

1. *F. excelsior* occasionally suffered frost damage and displays several phenological adaptation to flowering early in the season (figure 14, plates 3 and 4). Effective wind pollination is enabled by the early flowering before leaves unfold, and the problem (for entomophilous ancestors) of low insect numbers is avoided. *F. excelsior*'s lateral inflorescences present a morphological adaptation for flowering before the leaves unfold (from the apical bud, de Jong 1990, Wallander 2001).

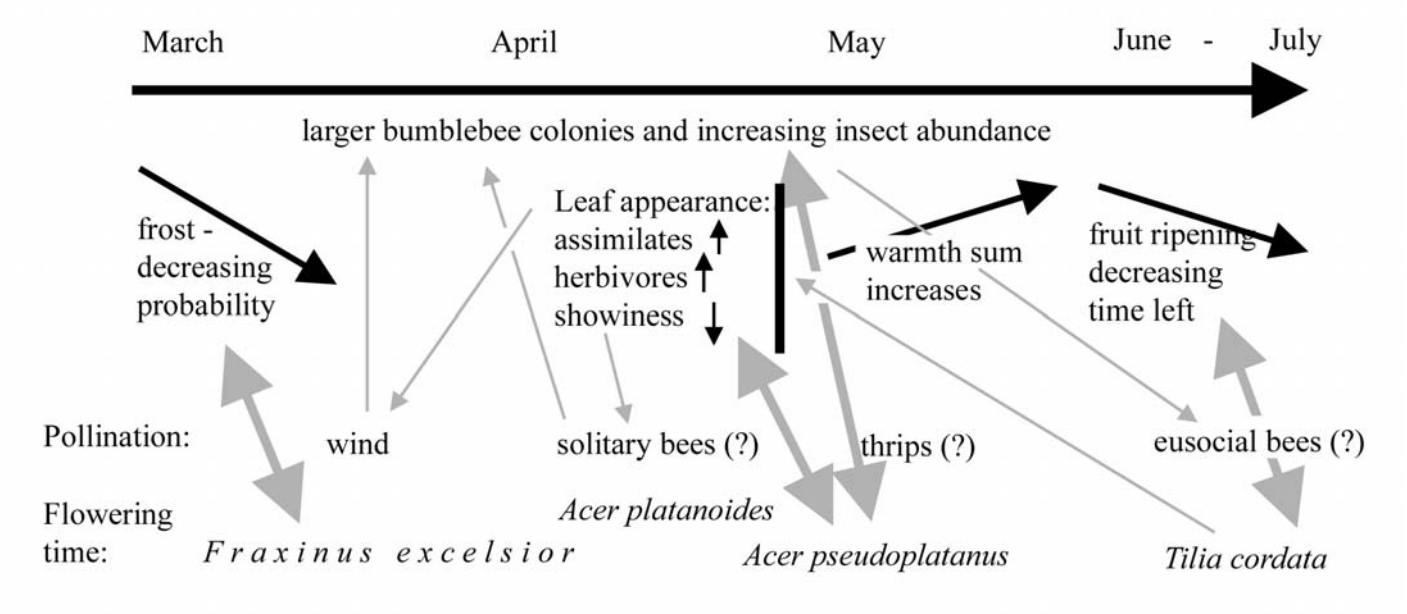

Figure 40: Flowering phenology and pollination of the studied species in relation to the main ecological factors during the flowering period. The time axis is from left to right, with the ecological factors and the tree species (after their flowering time) placed accordingly. The black arrows denote the temporal changes in the different ecological factors, the grey arrows represent the interactions between the reproductive biology of the species and the ecological factors: Double headed arrows denote a conflict, arrows headed at the species denote an ecological factor that promotes pollination, and the arrows headed at the ecological factors represent a resolution of a potential conflict. See text for discussion.

2. *T. cordata*'s late flowering brings with it the risk of an incomplete fruit development (Pigott 1981). A large enough warmth sum, on the other hand, is needed to enable pollen tube growth, limiting its flowering to a warm enough season (Pigott and Huntley 1981, Pigott 1981, 1989 and 1992). Its late flowering enables it to use bumblebees in a great number for pollination and flowering trees are conspicuous on the green background due to the inflorescence bracts.
3. *A. platanoides*'s flowering just before leaves in the forest unfold increases its showiness, and the species' typical low frequency (Haas 1933, Roloff and Pietzarka 1998, Seele 2004) and small flower number may still enable pollination by solitary bees. It is interesting that *A. platanioides* reaches a higher frequency in Europe only in association with *T. cordata* (in *Asperulae (odoratae) – Tilietum*, after Roloff and Pietzarka 1998), which is one of the most entomophilous forest trees in Europe. It may be worth checking if this is due to a higher bee population supported by this kind of forest.
4. *A. pseudoplatanus*' flowering just after leaves unfold causes a flowering tree to be optically indistinguishable from non-flowering trees, and possibly suffer much

herbivore damage (2005, results before table 10). The large number of flowers (a typically dominant species, large inflorescences) exceeds by far the pollination capacity of the present bees and flies (this may however depend on the site).

The low pollination and seed set levels in *A. pseudoplatanus* may thus be connected to its flowering time in relation to the unfolding of leaves and existing insect populations. The difference in pollination and seed set between protogynous and protandrous trees was tentatively explained by thrips as brood-site pollinators in the former. Floral traits such as flower number per tree, inflorescences size and pollen characteristics of *A. pseudoplatanus* are quite close to those of the anemophilous *F. excelsior*. The main difference between them is in flowering time, which relates to the insertion of the inflorescences on the twig (Ogata 1967).

It would be interesting to check if an evolutionary change with the following steps may be applicable for other species and habitats:

1. An entomophilous species becomes dominant in a habitat to an extent that its pollinators cannot effectively pollinate the large flower numbers (Cox 1991).
2. Brood-site pollinators become thus more effective than the original (larger) pollinators and select for even more flowers and more "anemophilous" characteristics. As the abundance of small insects may increase more quickly after the beginning of the vegetation period than that of the original larger insects, brood-site pollinators may commonly select for an earlier flowering.
3. Efficiency of wind pollination may then increase, and the species may become anemophilous.

Appropriate ecosystems that may support such a process and be interesting to study in this respect are dipterocarpous tropical forest, temperate and boreal heathes, *Artemisia* shrublands and the species gradient in *Espeletia* as well as *Thymelaea hirsuta* may also be cases in which the hypothesis can be tested (for references see introduction).

Gender separation, specialisation and small arthropods

The detailed study of the sexual systems of the species supports and refines the view of the differences between them as a gradient and points out the role of the rare androdioecious and heterodichogamous pathways to dioecy and possible selection pressures that drive them. Gender specialisation and a higher investment in the male function are common features of the studied trees, as is the importance of the role played by small arthropods in the process of gender separation.

The studied species fall into different qualitative categories of gender expression (figure 4a, Sage et al. 2005). Early flowering *F. excelsior* is functionally close to dioecy (evident on the bimodal distribution of functional gender, figures 9, 36), later flowering *Acer* spp. are monoecious and individual trees of *A. pseudoplatanus* differ in a gradual manner in their functional gender (figure 23a), and late flowering *T. cordata* has a majority of hermaphrodite flowers. The latter two species seem to tend to a further separation of gender - in *A. pseudoplatanus* heterodichogamy splits the sexual system, potentially enabling reproductive differences to occur between types and in *T. cordata* the number of male flowers per tree may depend on endogenous and exogenous factors that may induce further changes in the sexual system.

Dichogamy of about a week (and longer in *F. excelsior* and *A. pseudoplatanus*, few days in *T. cordata*) and synchrony of flowering time among the trees are conflicting tendencies, as the overlap of genders is crucial for successful pollination (Bawa 1983). The potential problem is confronted in *Acer* spp. by heterodichogamy, which has far-reaching consequences to the structure of the breeding system and in *T. cordata* by graduation of inflorescence unfolding, probably accompanied with much geitonogamy (see below, Fromm 2001). In *F. excelsior* it might have driven the male specialisation as the variable flowering time and pollination mode may increase the male-male competition to be the first to flower when female anthesis takes place. Evidence for this process can be seen in the altered pattern of male inflorescence unfolding.

Vegetative and generative differentiations accompany the separation of gender. In *F. excelsior* several phenological characters are different in trees of different gender as well as are tree size and the degree of gall infestation. In *A. pseudoplatanus*, trees of different gender sequences

differ in female flower number (the difference increasing with tree size), in tree size itself and possibly in the main pollinator. Fruit production is the largest in *F. excelsior*, in which gender separation and specialisation are developed to the largest extent, possibly indicating the adaptiveness of gender separation, wind pollination and early flowering in this ecological situation.

A higher investment in the male function was found in all the studied species. It is evident in *F. excelsior* in the higher grade of specialisation in males, in *A. pseudoplatanus* in the larger number of male flowers in respect to female flowers in both gender types (this ratio is higher than in the more entomophilous *A. platanoides*, figure 4b, Semm 1966) and in the occurrence of male trees, and in *T. cordata* in its andromonoecy. This common feature may relate to tree habit, pollination mechanisms or to flowering phenology and maybe to partial self-supply of the fruit, having green flight accessories, with assimilates (Bazzaz et al. 1979).

Small arthropods are intimately involved and may have a partial role in the gender separation in the studied species:

1. In *F. excelsior* gall mites infest males almost exclusively, a load that may limit further specialisation, be indifferently born by the trees, but may also accelerate male specialisation (Verdú, Gracía-Fayos and Gleiser 2004).
2. In *A. pseudoplatanus* thrips as brood-site pollinators may accentuate the female and male success in protogynous and protandrous trees (respectively), as well as practice a pressure toward earlier flowering which may lead to further specialisation of gender as wind pollination may become more effective. The type of pollinator may in general affect the relative male and female roles of gender sequence types in a heterodichogamous system (table 25).
3. Maleness in *T. cordata* flowers seems to be connected with floral infestation by gall midges in one of the two ways: (1) Infestation damages female function more than it damages male function, thus gall midges directly cause maleness (different flower forms relate to different timing of infestation and of parasitoid infestation of the gall midges). (2) Male flowers serve as preferred gall site for the midges, so that the tree spares damage to its hermaphrodite flowers (Pollak and Schwartz-Tzachor 2005 and see Bertin 1982). The interaction clearly needs further study.

Flowering phenology – dichogamy, synchrony, climatic effects and the vertical flowering pattern

The details of flowering phenology were found to be essential for the understanding of gender separation, pollination and fruit production in the studied species. The interplay of dichogamy and synchrony serves different purposes in the studied species at tree level, as does the unfolding process at inflorescence level. Both are further affected by the environmental factors – the exogenous climate and the endogenous physiological "awakening" of the trees in early spring.

It is conspicuous that the dichogamy in the species is gradual. *Acer* spp., flowering between the protogynous *F. excelsior* and the protandrous *T. cordata*, consist of a mix of the two types and the ratio seems to play an important role in the fitness of the individual trees (table 25). The two dichogamous modes correspond to the two pollination ecotypes (Fenster et al. 2004) represented by other floral traits as well, which is a unique character of the heterodichogamous system, and may apply to other such systems as well (Renner 2001). Synchrony plays a key role in the maintenance of dichogamy, affecting male specialisation and reproducing tree groups in *F. excelsior* (figure 13), the whole breeding system in *Acer* spp. (table 12) and the regulation of geitonogamy in *T. cordata* (figure 31c).

Inflorescence level phenology regulates of the effects of dichogamy. Protogyny in *F. excelsior* may enable selfing in hermaphrodite inflorescences in case of no pollination and is responsible for the "waiting phase" in male inflorescences (results after figure 11, plate 3, Tal 2003). Heterodichogamy is at inflorescence level in *Acer* spp. and it separates the population into two distinct groups with reciprocal pollination and the synchronisation of pauses inhibits selfing (tables 10 and 12, figure 24). The protandry in *T. cordata*, that suppresses selfing at flower level, mediates selfing at inflorescence level, due to the gradual unfolding of the inflorescences. These findings imply viewing the inflorescence as the basic functional unit in the breeding systems (Harder et al. 2004). Unfolding of inflorescences is differently connected to anthesis in the studied species. The unfolding process governs many aspects of flowering phenology in *F. excelsior* (determining both gradual flowering and weather protection figure 14, plates 3 and 4, Tal 2003). In *A. platanoides* it goes hand in hand with anthesis and gender changes (figures 17 and 19, plate 6, Haas 1933), and it is also responsible for the showiness of a flowering tree. In *A. pseudoplatanus* and *T. cordata* unfolding of the

inflorescences occurs mostly before anthesis and unfolding of floral parts are responsible for the regulation of flowering phenology (stigma lobe spreading, filament lengthening, tables 3 and 22, plates 2 and 7, Eisenhut 1957). South-north differences in phenology are most evident at inflorescence level of male *F. excelsior* (figure 14c, plate 3) and are weak at inflorescence level in *A. platanoides* (plate 6) and at tree level in *T. cordata* (figure 31b). The first and last instances were clearly correlated with sun irradiance (figures 44b and 45a in the appendix).

The durations of flowering (about a month per species) are similar among the species for full flowering years and decrease in years of partial flowering (figure 43 in the appendix). The duration of flowering of *F. excelsior* was the only one that differed between years of full flowering due to the influence of the weather. The climatic effects on flowering phenology comprise of several factors (for *F. excelsior* - end of winter and cold interruptions during flowering, table 29 and see appendix for further discussion), that are not readily predictable from the current evidence of climate change (Glaser 2001, Badeck et al. 2004, Cook et al. 2005, Menzel et al. 2005). The consequent flowering times were coupled with a decreasing sensitivity of flowering phenology to weather, as exemplified by the high sensitivity of *F. excelsior*, middle sensitivity of *A. platanoides*, small sensitivity of *A. pseudoplatanus* and vanishing sensitivity of *T. cordata* (figures 7, 12, 14, 31 and 43, table 29, plates 4 and 6). However, the main flowering period of each species was constant (figures 11, 24, 43, table 5, in accordance to Chuine et al. 2000 for other tree species), except for the extreme year 2006 in which the flowering periods of *F. excelsior* and *Acer* spp. have shifted two weeks and one week later, respectively.

Flowering in *F. excelsior* and *A. platanoides* proceeded from the lower part of the crown upwards and also from within the crown outwards (Tal 2003 and figure 19, respectively). The "down-upwards" pattern of flowering fades out in later flowering *A. pseudoplatanus* and *T. cordata* (table 13, results before figure 31). This flowering pattern overrides and may partly overcome the strong dichogamy in *F. excelsior* and *Acer* spp., Temperature and humidity gradients are small at the 10m scale in the forest before leaves unfold and become large only as the canopy greens (figure 44a in the appendix). Microclimatic effects of sun radiance are evident at the 1cm scale (figure 45a, plates 3,4 and 6) but cannot be readily drawn to explain the vertical pattern. Vertical differences in wind speed (Wilmers and Ellenberg 1986, Geiger et al. 1995, Nathan and Katul 2005) are probably not responsible for it either.

This flowering pattern may be caused by the gradual building up of sap flow in the trees in early spring. I couldn't find direct measurements of flow speed in the studied trees, but only indications, such as Huber's (1956) measurements for *Picea abies* showing a low flow speed in early spring, maximal below ½ meter per hour, and Essiamah's (1980, 1982) findings that sap in *A. pseudoplatanus* came two weeks later from a point 2.5m higher along the stem, and the hysteresis curves of flow velocity in Tyree and Zimmermann (2002) that indicate a strong dependence of flow velocity on temperature (the dependence on transpiration is irrelevant before leaves unfold). Also wood anatomical considerations indicate that transport speed is limited in *F. excelsior* and *A. platanoides* in early spring – the former is ring porous and thus build its new spring vessels late; and the latter flushes exceptionally early in relation to other diffuse porous species, possibly indicating lower transport effectivity (Lechowicz 1984 and 1995). Findings that support the hypothesis of limited transport as reason for the acropetalous and centrifugal flowering pattern are:

1. The strongest effect is early in the season, especially before leaves unfold, and it weakens towards summer.
2. The unfolding of leaves largely annihilates the pattern. It both indicates that sap has reached all twigs ends (indeed leaves unfolding in *F. excelsior* and *A. pseudoplatanus* followed a similar pattern, in the latter the flowering pattern is most evident at the beginning of flowering season, table 13), and leaves becoming sources of assimilates weakens the down-upwards dependency on resources.

However, the basic mechanisms of water transport are not fully understood, especially in the beginning of vegetation period (Tyree and Zimmermann 2002) and are controversial (Zimmermann et al. 2004). *Acer* spp. and *F. excelsior* also differ much in their behaviour at early spring, as the former have an intensive sap flow that is partially temperature dependant whereas the latter has no sap flow (Essiamah 1980 and 1982, Tyree and Zimmermann 2002), its flowering probably depends on local transport in the flowering twigs (Gill 1933) and possibly on an upwards transport of a small amount of water or hormones (Stephan Mayr, personal communication).

Pollination mode, intensity and patterns

The studied species range from anemophily to entomophily. The *Acer* spp., flowering between the early flowering anemophilous *F. excelsior* and late flowering mostly entomophilous *T. cordata*, contrast in their pollination strategies. *A. platanoides* with relatively few individuals and fewer flowers is bee pollinated, whereas the common *A. pseudoplatanus* with its numerous flowers seems to rely on brooding thrips as pollinators in this stand. The measurements of pollen diameter separate *F. excelsior* (below 25µ) and the other species (around 30µ) more distinctly than do the different literature data and in correspondence to the main difference in pollination mode. The pollination modes are to some extent indicated by the range of pollen to ovule ratios (Cruden and Miller-Ward 1981, Cruden 2000), calculated at inflorescence level, among the individual trees of each species, figure 4b). The inflorescence level was chosen as it is the basic phenological unit and as it allows the inclusion of the male to female ratio of diclinous species in a natural way. Male specialisation in *F. excelsior*, connected with anemophily, corresponds to very large P/O's. Protogynous *A. pseudoplatanus*, that were shown to benefit from the less exact thrips pollination (in respect to bee pollination, Cruden 2000) had higher P/O's than protandrous trees (table 25), and both *A. pseudoplatanus* and *T. cordata* that were shown to tend more to anemophily than *A. platanoides* also had higher P/O's (Eisenhut 1957, Hesse 1979a and c, Grube 1988, Paw U and Hotton 1989). The ratio of pollen number to stigma area seems to support the indications to pollination modes, but must be related to the pollen bearing area of the pollinator to enable conclusions (Cruden and Miller-Ward 1981, Cruden 2000, see also discussion of pollen group sizes).

A direct quantification of the contributions of bees, thrips and wind to pollination has failed because of technical difficulties. The comparison is thus restricted to the limited observations:

1. Bees: Collected pollen from male *F. excelsior*, probably pollinated *A. platanoides* (*Andrena* and *Bombus* spp.), were conspicuously seldom on *A. pseudoplatanus* and very abundant (mainly *Bombus* spp., also syrphid flies and others) on *T. cordata*.
2. Thrips and nitidulid beetles: Were found in *F. excelsior* inflorescence, and were abundant in inflorescence of the later flowering species (thrips – one species in *Acer* spp. and another in *T. cordata*, nitidulids – probably two generations of *Epuraea melanocephala* in *Acer* spp. and *T. cordata*, Thomas Wagner, personal communication). These insects are a part of a small food web around the flowers.

Thrips probably acted as the most effective pollinators of *A. pseudoplatanus*. Nitidulid beetles are known as pollinators (Proctor et al. 1996, Gottsberger 1999), but their role here was not checked.

3. Birds (*Parus caeruleus*) fed on insects in inflorescences of *F. excelsior* and *A. platanoides* (and opening buds of *A. pseudoplatanus*) as part of their early spring diet (Hudde 1993). They may regulate so florivore abundance, and in *F. excelsior* may act as secondary pollinators (one catch is however too few evidence). This possibility is interesting for further study as bird pollination in Europe is rare (Búrquez 1989, Ortega-Olivencia et al. 2005) and as the reward are insects in the flowers and not nectar. Squirrels fed on inflorescences of *Acer* spp., their role as pollinators may be anecdotal at most.

Pollination effectiveness was highest in *F. excelsior*, which had the most pollen on its stigmas and the strongest pollen tube competition, whereas *A. pseudoplatanus* and *T. cordata* had little pollen on the stigmas and medium or low pollen tube competition respectively (figures 15, 25 and 32, tables 8, 14 and results before figure 32). This comparison may be taken to show that wind pollination is more efficient for dominating temperate trees than entomophily, providing the driving force to the evolutionary change of pollination mode (detailed discussion and comparison to boreal forest in Smith et al. 1990). However caution should be taken due to the peculiarities of the stand and to the tremendous difficulty to encompass the variation of pollination among and within individuals, which is only touched upon in this study.

Groups of germinating pollen on stigmas in *A. pseudoplatanus* and *T. cordata* were similar in their small size and high frequency (results after table 14 and results before figure 32, respectively). In the former, group size and frequency are double, in the latter similar to those found by Rempe (1938) in the crown space of these trees. This indicates a pollination mode that does not concentrate much the pollen grains in relation to their grouping in the air. The number of grains per stigma is however much lower than expected from Rempe's findings, possibly due to spatial and temporal considerations (see discussion of the species). It is suggested that pollinators may be *a posteriori* distinguished using their "pollen traces" on the stigma, but this suggestion must be experimentally checked by observing "pollen traces" of insects in controlled pollinations.

Fruit and seed production and geitonogamy

Flowering and fruiting intensity were high and constant in *F. excelsior* but fluctuating in the other species. *F. excelsior* surpassed the other species in fruit and seed quantities. *T. cordata* approaches it only in the full fruiting year. This case of an annually fruiting anemophilous species versus biannually fruiting entomophilous species contrasts the theoretical association of wind pollination and masting (Tisch and Kelly 1998, Kelly and Sork 2002), but is probably caused by the different maturity levels among species' trees in the stand (appendix, tables 26 and 28). In *F. excelsior* and *T. cordata* few trees with the largest crown area produced more fruit, whereas in *A. pseudoplatanus* the yield was distributed more equally among the individual trees (probably due to the interferences of the distribution of tree size and of gender sequence, figure 23b). Seed set per fruit was high in *F. excelsior* and *T. cordata* but medium in the *Acer* spp.. The higher seed set in the protogynous *A. pseudoplatanus* trees than in the protandrous trees reflects the pollination intensity.

Vertical patterns in pollination, fruit and seeds were found in some trees and in others not, probably depending on details of flowering phenology, nutrient supply and constellation of neighbouring trees. The comparisons were too few to encompass the variability, but the following trends may be noted:

1. Pollination: In *F. excelsior* (Tal 2003) and *A. pseudoplatanus* pollination level was somewhat higher in the lower crown than in upper crown (possibly due to the vertical pattern of flowering). In *T. cordata* pollination level was higher in upper crown.
2. Fruit and seeds: In *Acer* spp. more fruit per infructescence was recorded in upper crown, seed per fruit were higher in upper crown of *A. pseudoplatanus* but was the same as in lower crown in *A. platanoides*. In *T. cordata* fruit per infructescence did not differ within the sun crown, but the seeds per fruit ratio is higher in upper crown.

The studied species are all self compatible to some extent, and individuals differ from each other in this respect, as reported in former studies (Fromm 2001, Morand-Prieur et al. 2003, Pandey 2005). Quantifying the role of selfing in the stand requires a genetical study, and is probably strongly decimated by inbreeding depression (Charlesworth and Charlesworth 1987). It is probable, regarding the flowering phenology, that much geitonogamy characterises *T. cordata* (Fromm 2001, see also Stephenson 1982), whereas in the other species geitonogamy is limited by the dichogamous patterns. Still, even in *T. cordata* the

strong reduction in seeds but not in fruit in 2005 (figure 35) may indicate the necessity of outcrossing. If indeed somatic mutations within individual trees are abundant (Klekowski and Godfrey 1989, de Jong et al. 1992, Gill et al. 1995), geitonogamy must be studied in a more differentiated way, namely separated to the flower, inflorescence, branch and main branch levels, as each may have different genetic consequences.

This study of the reproductive biology of the main tree species in the stand ends at fruit and seed production. However the implications of the reproductive aspect to the persistence (and evolution) of the species in the forest depend on the other aspects of their biology as well. In this stand the most frequent species at seedlings level are the *Acer* spp. (Schöne 2004), that were found to be inferior at seed production, and there are other studies in floodplain forests (Deiller et al. 2003) and in floral biology in general (Ollerton and Pellmyr 1982, Kochmer and Handel 1986, Eriksson and Bremer 1992, Ollerton and Lack 1992, Ricklefs and Renner 1994), that show that reproductive processes do not play an ecological or an evolutionary role under many circumstances. It is probably the most critical factor that determines the outcome of ecological and evolutionary interactions (Arber 1928, McAtee 1937, Stebbins 1970) and these critical factors probably vary in different ecological, geographical and paleobotanical ranges (e.g. Axelrod 1983, Wolfe and Tanai 1987). Still the results presented may contribute to the understanding of the factors that may play a role in cases in which the reproductive biology is such a factor.

The old problem to explain the evolution of gender separation and wind pollination could be for the first time studied in the crowns of mature trees, applying an interspecific ecological comparison. The main insight to this problem is the possible role of thrips as a pollinator abridging the change from insect to wind pollination.

The study underlines the complexity of such a change in the reproductive biology, and the interdependency of its characteristics among themselves and upon a variety of abiotic and biotic ecological factors. The complexity is also exemplified for each species for itself, and inspection of processes in the canopy revealed a host of new factors in their reproductive biology. It implies that precaution should be taken in two fields of current research: (1) Genetic studies of tree reproduction must relate to the structure and functioning of the breeding system in order to reach meaningful results. (2) Effects of climate change on tree reproduction and phenology cannot be simply extrapolated, but must include an analysis of the interdependent factors.

Themes for further study are:

1. Small insect pollination or brood-site pollination as an intermediate state in the transition from entomophily to anemophily – is it true for other habitats?
2. Can pollinators be *a posteriori* distinguished using their "pollen traces" of the stigma (experimental manipulation and review of literature)?
3. *Fraxinus excelsior* – physiology of flower gender determination. – What are the climatic effects (manipulation using covers), what is the effect of the gall mites (hormonal intervention?)?
4. Study of thrips behaviour in relation to pollination in *Acer pseudoplatanus*.
5. *Tilia cordata* – Tree control of gender, dynamics of gall midge and their parasitoids.

Summary

The study compares the reproductive biology of *Fraxinus excelsior* (ash), *Acer platanoides* (Norway maple), *Acer pseudoplatanus* (sycamore maple) and *Tilia cordata* (small-leaved lime) in the temperate deciduous floodplain forest of Leipzig. Its novelty is the study of the crowns of mature trees in a semi-natural forest, as well as the comparison between genera from an ecological point of view.

Fraxinus and *Acer* are renown for their diverse sexual systems and pollination modes, but they and *Tilia* origin from hermaphrodite entomophilous (insect pollinated) plant families. Their studied species are typical for temperate deciduous forests and together they constitute gradients in the grade of gender separation, flowering phenology and pollination modes. The aim of this study is to understand the ecological interplay of these factors within the species and to compare the reproductive strategies among them.

Leipzig's floodplain forest is deciduous and species-rich. Since ca. 150 years its silvicultural use has been abandoned, and the trees were allowed to grow higher. At the same time flooding was regulated and the forest has become drier. The maturity of the stand and its natural species constitution may render it a semi-natural forest. The crane plot is located at the northern edge of one of its oldest nature reserves.

The LAK canopy crane enabled a frequent, non-distructive scrutiny of ca. 200 mature canopy trees of these species at all reproductive stages, which yielded a detailed description of the reproductive processes within individual crowns and their intraspecific variation, accompanied by structural and microclimatic measurements. Novel findings are the new definition of the sexual systems of *Fraxinus excelsior* and *Tilia cordata* as dioecy and andromonoecy respectively, the probable thrips pollination in *Acer pseudoplatanus* and new insights to the functioning of its heterodichogamous sexual system (reciprocal male-first and female-first flowering individuals), as well as the description of floral phenological patterns within the crowns. The ecological comparison discusses the intricacies of the seemingly simple process of gender separation and transition to anemophily (wind pollination), in which floral phenological details and small arthropods seem to play an important role.

The crane was extensively used it the study. Gender distribution was scrutinized every year and phenological stages at flower, inflorescence and tree levels were defined, checked every one to four days during the flowering period, which extended from March to July (the species flower consequently) and quantitatively estimated, coping with the large dimensions and number of the trees. Pollination (germinating pollen on the stigmas and pollen tubes in the styles) was studied using fluorescence microscopy and insects in inflorescences (collected with minimal disturbance) were counted and sent to identification. Fruits were pluck in September from complete branches, counted and checked for the existence of seeds. Special attention was given to vertical gradients in the crown of all characters. Correlations between gender distribution, flowering phenology, pollination and fruit were analysed.

Fraxinus excelsior is morphologically polygamous but functionally dioecious. Individual trees were categorised as either male, male-biased hermaphrodite, balanced hermaphrodite, female-biased hermaphrodite or female (presenting some adjustment of gender between neighbouring categories that are correlated with the weather) but the two former categories reproduce through pollen, the latter three categories reproduce through ovules. The border between males and females is clearly defined in the aspects: Tree size, flowering frequency and intensity, twig and inflorescence morphology, several phenological patterns at inflorescence level, gall infestation and fruit production. Dioecy seems to have evolved through the rare androdioecious pathway as males are more specialised than females.

Tilia cordata, regarded as hermaphrodite, was actually found to be andromonoecious as its trees had many staminate flowers. Additionally the trees had formerly not described gall flowers inflicted by gall midges, and flowers with a varying grade of pistil damage or reduction. The frequencies of these flower types depended in different ways on the flowering stage of the trees, suggesting that they origin from an interplay of sexual allocation patterns in the tree, the gall midges and their parasitoids

Acer pseudoplatanus trees are monoecious and flower at inflorescence level either male and then female (protandrous) or female and then male (protogynous), all inflorescences in accord. The flowering phenology of the two types was synchronised and reciprocal, so that trees of the one type were responsible for most of the pollination of the trees of the other type. These two types differed in further aspects: Protandrous trees were more numerous (3:1), had more female flowers (2-3:1), had much less pollen on their stigmas (1:15) and had a much

lower seed to fruit ratio (1:3-4, indeed some of them bore ten thousands of to 95% empty fruit). Bees and flies were rarely observed on the flowers, and the proportion of stigmas with pollen was significantly correlated with the number of adult thrips (*Taeniothrips inconsequens*) per inflorescences in the same probe (1:2-3 between the types). This suggests thrips as pollinators of *Acer pseudoplatanus* in the stand, and may explain the high seed set in the protogynous trees as related to the activity of thrips at the beginning of the flowering period (looking for mates and brood sites). When protandrous trees flower female, the thrips population in the inflorescences consisted mostly of larvae. A theoretical calculation demonstrates that the functional gender of each type critically depends on the efficiency of pollen transport. Moreover, the existence of two reciprocal types may be regarded as a natural experiment in pollination efficiency with numeral relations and pollinator availability being the main parameters.

Flower phenological differences among the species were that *Fraxinus excelsior* flowered every year in a constant intensity, whereas *Acer* spp. and *Tilia cordata* flowered in a strongly fluctuating intensity and that in contrast the total duration of flowering was constant in the latter species but changed drastically between years in *Fraxinus excelsior,* depending on the weather. Its flowering was sensitive to the timing of warm and cold periods in early spring, was easily manipulated by covering the twigs and frost damages were not infrequent but somewhat countered by the pattern of inflorescence unfolding. Different measures of synchrony of the individual trees were calculated and the implications of staggered versus clumped phenology to the gene flow in the population are discussed. The vertical flowering pattern – from lower crown upwards and from within the crown outwards (acropetalous and centrifugal) – prevailed and was conspicuous in the early flowering *Fraxinus excelsior* and *Acer platanoides*, was partially found or absent in the later flowering *Acer pseudoplatanus* and *Tilia cordata* (respectively). This pattern did not correspond to climatic gradients in the forest, which built up only as the leaves unfold, but it may reflect the "physiological awakening" of the trees.

The most prolific fruit producer was *Fraxinus excelsior*, which had a relatively constant crop of one to one and a half million fruit per hectare per year. *Tilia cordata* followed with a somewhat smaller crop but only on the year of full flowering. In both species few trees with the largest crown area produced most fruit. *Acer pseudoplatanus* was inferior in fruit and even

more in seed quantity (the latter reaching merely 200,000 in the full flowering year), and the crop was more evenly distributed among individual trees.

The different combinations of sexual system and pollination mode are discussed in relation to the time of flowering, in the ecological context of abiotic factors (frost and the duration of vegetation period) and biotic factors (time of unfolding of leaves with its different implications and the increasing number of insects during the flowering season). *Fraxinus excelsior* is wind pollinated, a factor which promotes gender separation, and its flowering before leaves unfold make this pollination mode effective. However, the flowering is susceptible to climatic hazards, which are encountered (or exemplified) by the phenological sensitivity to weather. A late flowering tree like *Tilia cordata* on the other hand may be pollinated by large insect populations (e.g. bumblebee colonies) but may be limited in fruit ripening by the short part of the vegetation period left for fruit ripening. Gender separation in *Tilia cordata* is in an initial stage. The two *Acer* spp. have contrasting reproductive traits. *Acer platanoides* is insect pollinated and flowers just before leaves unfold, enhancing their showiness and importance at nutrient resource. It is infrequent and has fewer female flowers than its congener, and thus may be effectively pollinated by solitary bees of early spring. The little later flowering *Acer pseudoplatanus* is much more abundant and has numerous greenish flowers that are less discernable from leaves. Its inflorescence and floral morphology show a tendency towards wind pollination, but its efficiency is impeded by foliage. Indeed, it suffers from low pollination and low seed set.

But not the protogynous type that is probably thrips pollinated. Thrips may be seen as an insect pollinator that requires morphological characteristics, which are usually assigned to wind pollination (e.g. many flowers, much pollen which is not very sticky) and its functioning as a brood-site pollinator may create a natural pressure towards earlier female flowering. The failing trait for *Acer pseudoplatanus* to be wind pollinated seems to be the flowering before leaves unfold, involving a shift from terminal to lateral insertion of the inflorescences on the twig, a shift which is a basic distinctive feature between wind and insect pollinated species of the genera *Fraxinus* and *Acer*. Thrips pollination may thus function as an intermediate pollination system driving the transition from bee to wind pollination in mass flowering plants.

Zusammenfassung

Die vorliegende Studie vergleicht die reproduktive Biologie, inklusiv die Blühphänologie, von *Fraxinus excelsior* (Esche), *Acer platanoides* (Spitzahorn), *Acer pseudoplatanus* (Bergahorn) and *Tilia cordata* (Winterlinde) im Leipziger Auenwald. *Fraxinus* und *Acer* sind für ihre Diversität an Sexualsystemen und Betäubungsmodi bekannt, aber sie stammen, wie *Tilia* auch, aus zwittrigen, insektenbestäubten Familien. Ihre Arten sind für die laubabwerfenden Wälder typisch, und zusammen zeigen sie Gradienten bei der Geschlechtstrennung, Blühphänologie und Bestäubungsweise. Ziel dieser Studie war es, das Wechselspiel dieser Faktoren im Ökosystem Wald besser zu verstehen.

Der Leipziger Auwaldkran ermöglichte eine regelmäßige und schadenfreie Untersuchung von ca. 200 ausgewachsenen Bäumen im Kronendach während aller Stadien der Reproduktion. Das Alter und die natürliche Artenzusammensetzung des Waldes lassen ihn als naturnahe gelten. Der Kransstandort liegt an der nördlichen Grenze einer seiner ältesten Naturschutzgebiete. Der Kran wurde in dieser Studie extensiv genutzt. Die Geschlechtsverteilung wurde in Detail überprüft und die blühphänologischen Stadien wurden regelmäßig (1-4 Tage) während der Blühzeiten (März bis Juli) aufgenommen. Die Beschreibung war grundsätzlich quantitativ trotz Größe und Anzahl der Bäume. Das Geschlecht der Bäume wurde jedes Jahr neu erfasst, um Änderungen wahrzunehmen, und die Blühphänologie wurde bei *F. excelsior* und *A. pseudoplatanus* in Detail analysiert. Der Bestäubungsgrad und die Insekten in den Blütenständen wurden durch möglichst störungsfreies Sammeln der Blütenstände und durch fluoreszenz-mikroskopische Untersuchung der Pollenkeimung bzw. Zählung und Bestimmung studiert. Die Früchte wurden in September gesammelt, gezählt und auf Samenausbildung geprüft. Besonderes Augenmerk wurde auf vertikale Gefälle der Messgrößen innerhalb der einzelnen Kronen gerichtet. Die Geschlechtsverteilung, Blühphänologie, Bestäubungsgrad und Fruchtsatz wurden im Bezug aufeinander korreliert und analysiert. Die strukturellen und mikroklimatischen Rahmenbedingungen wurden ebenfalls erfasst.

Fraxinus excelsior Bäume wurden als männlich, männliche Zwitter, ausgewogene Zwitter, weibliche Zwitter oder weiblich klassifiziert, wobei gewisse Änderung des Geschlechts unter benachbarte Kategorien im Zusammenhang mit der Witterung beobachtet werden konnte.

Untersuchung des Fruchtsatzes und der Pollenproduktion ergaben, dass die ersten zwei Gruppen als männlich, und die letzten drei als weiblich angesehen werden müssen, sodass das Sexualsystem funktionell diözisch ist. Männliche und weibliche Bäume unterscheiden sich durch: Baumgröße, Blühfrequenz und –intensität, Morphologie der Zweige und der Infloreszenzen, mehrere blühphänologische Muster auf der Blütenstandsebene, Gallenbefall und Fruchtmenge. Da die männlichen Bäume stärker als die weiblichen Bäume spezialisiert sind, scheint sich die Diözie über die seltene Androdiözie evolviert zu haben.

Tilia cordata Bäume weisen viele männliche Blüten auf, sodass diese "zwittrige" Art eigentlich als andromonözisch anzusprechen ist. Sie hat männliche Blüten, Gallblüten (durch Gallmücken verursacht, neu beschrieben) und Blüten mit zu unterschiedlichem Grad beschädigten Pistil. Die Abhängigkeit der Häufigkeit dieser Blütenformen vom Blühgrad im Baum war unterschiedlich, was auf einem Zusammenspiel der baumeigenen Sexualverteilung, der Gallmücken und ihren Parasitoiden hindeutet.

Acer pseudoplatanus ist einhäusig, und blühte auf Blütenstandsebene synchron entweder vormännlich (protandrisch) oder vorweiblich (protogyn), sodass die Population funktionell zeitweise diözisch ist (heterodichogam). Der reziproke baumbezogene Wechsel dieser zwei Typen bewirkte, dass Bäume von dem einen Typ fast ausschließlich für die Bestäubung der Bäume des anderen Typs verantwortlich waren. Die beiden Typen unterschieden sich auch in folgender Hinsicht: Vormännliche Bäume waren in der Mehrzahl (3:1), hatten mehrere weibliche Blüten pro Blütenstand (2-3:1), bekamen weitaus weniger Pollen auf ihren Narben (1:15) und produzierten weitaus weniger Samen per Frucht (1:3-4, einige von ihnen hatten zig Tausende von bis zu 95% leere Früchte). Es wurden nur wenige Bienen und Fliegen an den Blüten beobachtet, aber der Anteil der Narben mit Pollen korrelierte signifikant mit der Anzahl von adulten Thrips (*Taeniothrips inconsequens*), die sich im Blütenstand vermehren. Dies deutet auf Thrips als die effektiven Bestäuber von *A. pseudoplatanus* im Bestand hin, und könnte den hohen Samenansatz in den vorweiblichen Bäumen als Konsequenz der hohen Aktivität der Thrips am Anfang der Blühperiode (aufgrund der Partner- und Brutplatzsuche) erklären. Wenn die vormännlichen Bäume weiblich zu blühen anfingen, bestand die Thripspopulation in den Blütenständen vorwiegend aus Larven. Die Asymmetrie in Baum- und Blütenzahl verursachte ein unterschiedliches Verhältnis zwischen männlicher und weiblicher Blütenzahl in den zwei Blühphasen im Bestand. Dieses Verhältnis, und die Effizienz der Bestäuber in jedem Stadium wurden mittels eines einfachen Modells

verallgemeinert. Das Modell zeigte, dass das Geschlecht eines Typs gegenüber dem anderen stark von der Effektivität der Bestäubung abhängt und dass das Bestehen der gegenseitig bestäubenden Typen eine Anpassung an unterschiedlichen Bestäuberspektra ermöglichen könnte.

Im Vergleich zu den anderen Arten blühte *F. excelsior* jedes Jahr in etwa der gleichen Intensität, während bei *Acer* spp. und *T. cordata* sich die Blühintensität stark vom Jahr zu Jahr änderte. Die Dauer des Blühens blieb bei den letztgenannten Arten ungefähr konstant, während sie bei *F. excelsior* sehr in Abhängigkeit vom Wetter schwankte. Die Blühphänologie von *F. excelsior* reagierte empfindlich auf kalten und warmen Perioden im Frühjahr, und konnte leicht durch Verhüllung der Zweige manipuliert werden. *F. excelsior* Bäume litten gelegentlich unter Frostschäden, die allerdings durch die Muster der Blütenstandsentfaltung gemildert wurden. Ein Maß für die Synchronität der einzelnen Bäume wurde berechnet und die Auswirkung von gestaffelter gegenüber synchroner Blühphänologie wurde diskutiert. Bei *F. excelsior* und *A. platanoides* dominierten blühphänologische Unterschiede in den Kronen, die entlang von Gradienten (von unten nach oben und von innen nach außen) deutlich waren. Diese traten bei *A. pseudoplatanus* nur teilweise und bei *T. cordata* gar nicht auf. Die beobachteten Gradienten korrelierten nicht mit dem mikroklimatischen Gefälle im Wald (die erst nach der Laubentfaltung gebildet wurde), möglicherweise hängen sie mit dem „physiologischen Aufwachen“ der Bäume in Frühjahr zusammen.

F. excelsior war die fruchtbarste Art im Bestand, mit einem ziemlich regelmäßigen Ertrag von etwa ein bis zu anderthalb Millionen Früchte pro Hektar und Jahr. *T. cordata* folgte mit einem etwas niedrigeren Höchstertrag, aber nur in dem Jahr mit maximaler Blühintensität. In beiden Arten waren es wenige Bäume mit der größten Kronenfläche, die den Großteil der Früchte im Bestand produzierten. *A. pseudoplatanus* erzeugte wesentlich weniger Früchte, und noch weniger Samen (sie erreichen nur 200.000 pro Hektar und Jahr in dem Jahr mit maximaler Blühintensität), und der Ertrag war gleichmäßiger unter den einzelnen Bäumen verteilt.

Die Sexualsysteme und Bestäubungsmodi wurden auch im ökologischen Kontext verglichen. Dabei wurden sowohl die abiotischen Faktoren, wie Frost und Dauer der Vegetationsperiode, als auch biologische Faktoren wie die Zeit der Laubentfaltung mit ihren unterschiedlichen Folgen und die ansteigende Anzahl der Insekten im Wald, im Bezug auf die Blühzeit

berücksichtigt. *Fraxinus excelsior* ist windbestäubt, ein Modus, der die Geschlechtstrennung begünstigt, und wird durch das Blühen vor Laubentfaltung effektiv. Eine komplexe Blühphänologie schwächte die Gefahr von Frostschäden ab und veranschaulichte die starke Abhängigkeit der Blühvorgänge vom Mikroklima. Im Gegensatz dazu, kann ein spät blühender Baum wie *T. cordata* durch die große vorhandene Insektenpopulation (z.B. Hummeln) effektiv bestäubt werden, die jahreszeitlich späte Blüte verkürzt jedoch die verbleibende Zeit für die Fruchtreife. Die Geschlechtstrennung ist dementsprechend bei *T. cordata* unvollständig. Die beiden *Acer* Arten haben gegensätzliche reproduktive Merkmale. *A. platanoides* ist insektenbestäubt und blüht kurz vor der Laubentfaltung, wodurch die Auffälligkeit seiner Blüten erhöht wird. Sie ist seltener und hat weniger Blüten im Blütenstand als ihre Gattungsverwandte, und dadurch effektiv durch solitäre Bienen im Frühjahr bestäubt werden kann. Die etwas später blühende Art *A. pseudoplatanus* ist zahlreicher an Individuen und hat sehr viele grünliche Blüten, die schlecht von den Blättern zu unterscheiden sind. Die Morphologie der Blütenstände, der Blüten und der Pollen zeigt eine Entwicklungsrichtung zur Windbestäubung, deren Effizienz jedoch durch das Laub stark beeinträchtigt wird. In der Tat, litt *A. pseudoplatanus* im Bestand unter schwacher Bestäubung und niedrigem Samensatz.

Dies trifft jedoch nicht auf dem vorweiblichen Typus zu, der wahrscheinlich durch Thrips bestäubt wird. Thrips als bestäubende Insekten sind bei Blüten mit morphologischen Merkmalen effektiv, die üblicherweise mit Windbestäubung in Verbindung gebracht werden (wie eine große Anzahl von Blüten, sehr viel staubige Pollen) und ihre Tätigkeit als Brutplatzbestäuber könnte einen Selektionsdruck in Richtung früheres Blühen ausüben. Wenn *A. pseudoplatanus* vor der Laubentfaltung blühte, könnte sie effektiv durch den Wind bestäubt werden. Dies benötigt eine Verlagerung der Blütenstandknospen am Zweig von einer terminalen zu einer lateralen Position, die in der Tat ein wesentliches Unterscheidungsmerkmal zwischen wind- und insektbestäubten Arten der Gattungen *Fraxinus* und *Acer* ist. Thripsbestäubung könnte also als eine Zwischenstufe im Übergang von Insekt- zu Windbestäubung betrachtet werden und diesen Übergang besser erklären.

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Appendix and plates

The appendix describes shortly the study of structure, climate and microclimate in the stand, which I did as background to my main aim, the reproduction of the trees. I present here only the main results that are relevant to the main subject and remark their relevance. A study of genetic variability of *F. excelsior*, that is underway in collaborration with the Max Plank Institute for Limnology and the Hamburg University is also shortly presented. Afterwards color plates illustrating the themes of the study are presented.

Structure

Structure of the study site

A forest's canopy is a three dimensional space made up of crowded structures that may be analysed at different scales (Bongers 2001) – whole canopy (Birnbaum 2001), single tree crowns (Trichon 2001), branches (Frech et al. 2003) and leaves (Hutchison et al. 1986). The canopy is the basic life supporting matrix and its structure is thus a basic parameter for all organisms living in it (Norman and Campbell 1989). After two main steps of description of the canopy of LAK's plot have been taken – namely the recording of all trees in it, their stem diameter and height (Seele 2004) and the careful measurement of the canopy's upper surface (Rohrschneider, in press), these data may be integrated and the stand structure at a smaller scale may be studied.

Data to tree height and stem diameter were taken from Seele (2004). Crown area was assessed using an air photo of the stand from 2001, which is almost orthogonal (Markus Rohrschneider, personal communication). Each crown was outlined and identified (exact borders were determined in the forest using the crane). Crown area was assessed by comparing it to a scaled template of circles, ellipses and quadrates of different sizes using Photoshop®. The crown area was assessed in steps of $5m^2$ for small areas (up to 60 m^2), and $10m^2$ for larger areas. Crown area was measured for 259 trees (96% of ca. 270 canopy trees in the plot, overall there are 941 trees with stem diameter larger than 5 cm in the plot), including

large trees at the periphery of the plot. Total canopy area included is 1.2 ha (80% of the plot) as gaps were not included in the analysis.

The forest has been used by man since 650 years at least (Lange 1959) using different forestry practices. The major changes it underwent in the last 150 years are (Gläser 2001, Sickert 2003b):

1. Being left to grow higher by abandoning the practice of cutting down all trees but oaks every 10-15 years (figure 39, Lange 1959).
2. River regulation reduced and then prohibited regular flooding of the forest, thus drying it gradually.

These influences resulted in a higher forest with full canopy closure (Sickert 2003b) upcoming of the tree species *F. excelsior* and *Acer* spp. (see also Volk 2002), mainly *A. pseudoplatanus*, which are, together with *T. cordata* the dominating crown species of the study site (Seele 2004).

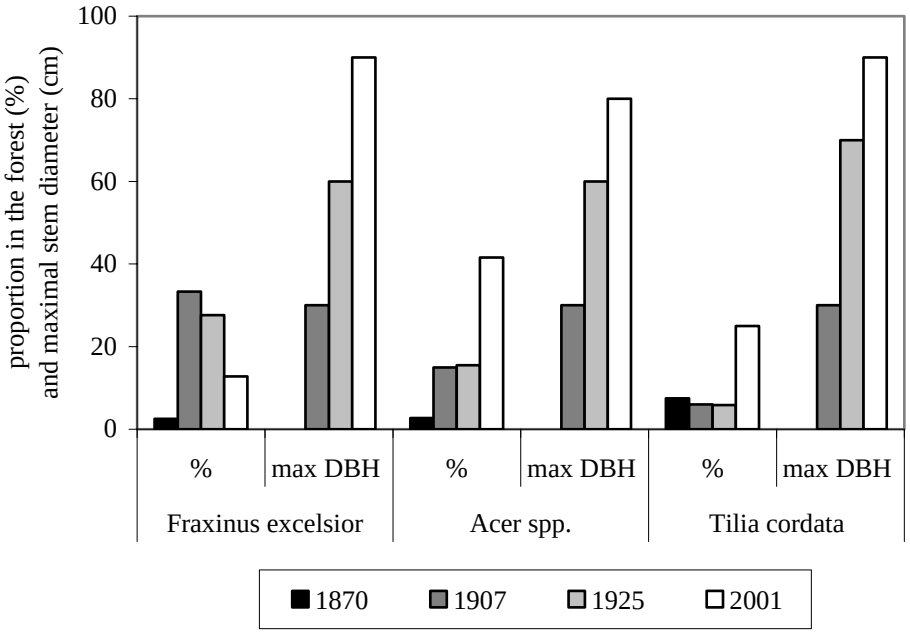


Figure 2: The development of the frequency and maximal stem diameter of the main studied species. Data for 1870-1925 from Lange (1959), and for 2001 from Seele (2004).

The upper surface of the canopy is quite clearly structured and could be separated into groups of trees, and these groups were classified in four categories (patch types): Highest groups with the largest trees (type 3, “climax”); intermediate-high groups (type 2, “older”); intermediate low groups (type 1, “younger”); and low groups which were actually young trees filling gaps

(type 0, “not closed”, gaps are not yet included in the classification). The definition of the groups was done in the forest, during the last two years of study, and was in most cases easy to make, as the structures were quite salient (plate 1, 21 trees were left out, most of them as being in gaps, some as border cases). An analysis of the sizes of the tree in the groups showed that the patches are distinct from each other in their tree composition and tree sizes. All patch types differ from each other in the heights, dbh’s and crown area of their trees significantly (table 26, Kruskal-Wallis one way analysis of variance on ranks $p<0.0001$, all pairwise significantly different (Dunn's method, $p<0.05$) except types 1 and 0).

Table 26: Crown area, height and stem diameter of 238 canopy trees after the patch type they belong to (plate 1).

patch type		3, climax	2, older	1, younger	0, not closed
number in the plot		9	7	6	1
total area (ha)		0.55	0.48	0.18	0.02
number of trees		54	81	87	16
average crown area per tree (m^2)		101	59	21	13
median tree height (m)		31.4	29.5	25.8	21
median stem diameter (dbh, cm)		70	52	32	19
proportion of tree species	*F. excelsior*	79%	28%	30%	
	A. pseudoplatanus	0	39%	37%	
	T. cordata	5%	14%	18%	
	others (see text)	16%	19%	15%	

F. excelsior dominates the most developed patch type (probably reflecting the strong increase in frequency in 1907 in figure 41), but shares the dominance with *A. pseudoplatanus* and *T. cordata* in the other types. *Quercus robur* makes further 11% of patch type 3 and is less frequent in the other types. In patch types 2 and 1 *Carpinus betulus* makes 6% and 3%, respectively. Other indigenous species together (mostly *A. platanoides*) make 5%, 6%, 4%, and introduced species together make 0, 6%, 9% (in types 3, 2 and 1/0 respectively), i.e. the latter increase in frequency as younger trees are taken into account.

Two qualitative characteristics of patches of type 3 are: 1. Within the patch - some trees are oblique; 2. On the patch boundary – some neighbouring trees have their main growth axis within the crown of a larger tree of the patch, and survive although their top is being repeatedly broken.

The trees in the plot are canopy trees starting from 50-70cm stem diameter and 27-28m height. 70% of the canopy trees have a crown area up to 50m^2. The histograms of stem diameter and tree height are quite flat – in the middle region the number of trees does not change much with stem diameter and tree height. In contrast, the histogram of crown area has a marked peak at low areas and a long tail to the right. This histogram is both more skew and more leptokurtic than the former two (skewness and kurtosis for the crown area histogram were 1.6 and 2.5, whereas for stem diameter they were 1.0 and 2.2, and for the tree height they were –0.7 (skew to the right) and –0.24).

Tree size parameters were significantly correlated with each other (table 27) and a linear regression was fitted to them, although a finer analysis may find a better fit to different curve types (Frech 2006, figure 42).

Table 27: Correlation of crown size of all canopy trees and of twig number in the largest ashes with other dimensional parameters of the trees (height and stem diameter – DBH).

Comparison	correlation[3]	linear regression[4]
crown size and stem diameter[1]	0.8	Crown area = -31 + 1.68 · DBH
crown size and tree height[1]	0.7	Crown area = -155 + 7.5 · Height
twig number and crown size[2]	0.8	Twig no. = 367 + 8.7 · Crown area
twig number and stem diameter[2]	0.7	Twig no. = -671 + 29.9 · DBH
twig number and tree height[2]	0.4	Twig no. = -3020 + 137 · Height

[1] for 258 canopy trees

[2] for 44 canopy *F. excelsior*.

[3] Spearman rank sum coefficient, $p<0.0001$ for all except ash twig number and tree height $p=0.007$.

[4] For slope and constant $p<0.001$, except constants for twig numbers ($p=0.003$, $p=0.024$, $p=0.06$ respectively) and the slope for twigs versus tree height ($p=0.01$).

A. pseudoplatanus trees are mostly of stem diameter 30-70cm and height 23-30m, some of them are smaller (around 20cm stem diameter and 20m height). In *F. excelsior* the trees' separation into two groups is pronounced – a large group of 30-32m height and stem diameter ranging 40-95cm and a smaller group of trees around 25m high and 25cm stem diameter. Also in *T. cordata* the trees may be easily separated into two groups – one around 30m height and

ranging 50-95cm in stem diameter, and the other around 25m height and 30cm stem diameter (figure 42).

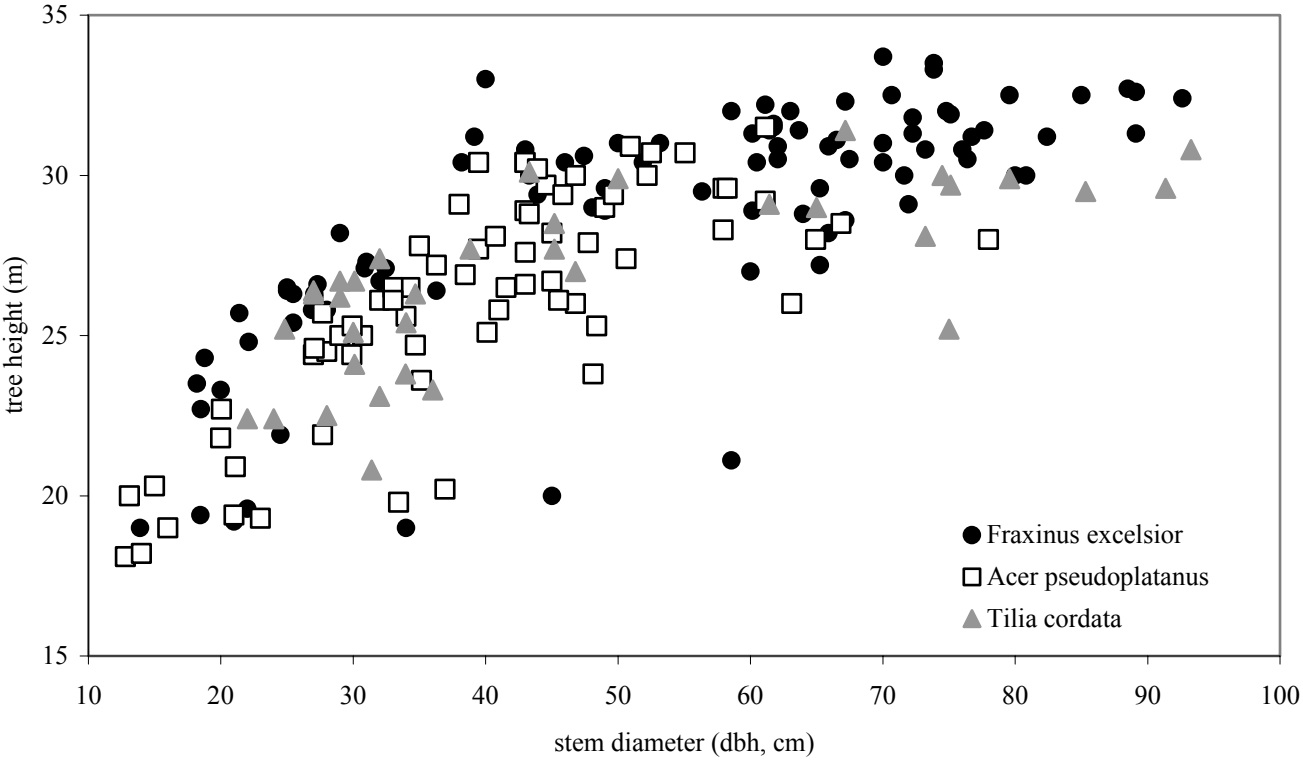


Figure 42: Sizes of the canopy trees of the three main studied species (202 trees, all of them were flower biologically studied).

F. excelsior and *A. pseudoplatanus* differ in the form the crown area depends on stem diameter and height. Crown area in *F. excelsior* increases two times stronger than in *A. pseudoplatanus* in relation to stem diameter and three times stronger in relation to tree height. This reflects their being dominant as an "upper layer" of the canopy (older trees). Crown area in *T. cordata* relates to stem diameter like *A. pseudoplatanus* and relates to height as in *F. excelsior* (table 28).

Table 28: Regression coefficients for the dependency of crown area (**c.a.**, m^2) on stem diameter (**dbh**, cm) and tree height (m) for the three dominating species in the plot. The constant to slope ratio roughly represents the minimal measure (height or stem diameter) for a tree to be a canopy tree (c.a.=0).

species (number of trees)	stem diameter (dbh, cm)	constant to slope	tree height (m)	constant to slope
Fraxinus excelsior (100)	c.a.=-36+2.0·dbh	18cm	c.a.=-188+8.9·height	21m
Acer pseudoplatanus (77)	c.a.=-16+1.1·dbh	15cm	c.a.= -53+3.1·height	17m
Tilia cordata (35)	c.a.=-19+1.2·dbh	16cm	c.a.=-172+7.9·height	22m
For all slopes $p<0.001$, for all constants $p<0.05$.				

The method for measuring the crown area is a manual version of studies like Trichon (2001) or Fuchs (2003), and as in these studies it should be noted that this area is only the one seen from above and not shaded by neighbours. The real tree crown area may be much larger, especially in species that habitually grow below the largest canopy tree, in the stand this case is typical to *Carpinus betulus* and to some extent to *Tilia cordata*, especially below *Fraxinus excelsior* (observation, Annika Frech personal communication).

Crown form is currently analysed in collaboration with Markus Rohrschneider. The trees of the climax patch seem more eccentric in respect to the stem location than trees of lower patches, an eccentricity that results either from obliqueness of trees (due to long time competition among trees with steadily increasing crown area) or from displacement of the crown main mass to exploit adjacent gaps.

The patches described are clearly distinguishable and differ from each other in many structural parameters. This most probably represents the succession in the development of the forest under the strong human impact (figure 41, Lange 1959, Sickert 2003b). For example the *F. excelsior* dominated patch type 3 probably goes back to the change in forestry practices around 1870 (Gläser 2001) and second world war bombing might have cleared smaller areas that could have been the basis for the patches of type 1. The stand is however too small to study the relation of patchiness to the species affiliation of the trees (Frelich et al. 1998).

The patchy structure of the plot and the strong correlation may be practically used to widen the data base on the forest – the regressions may be used to complete data that is available from ground measurements (stem diameter, stem density, coarsely tree height) as well as data

available from aerial photos (crown area and form, coarsely tree height) and so may serve as a basis to gain more information on structural parameters of Leipzig's floodplain forest (Andreas Sickert, personal communication). The data may also be used to calibrate a simulation of the flood plain forest's growth along lines similar to Neuert et al. (2001, Volker Grimm and Andreas Huth, personal communication), or by other model types (Bugmann 2001).

Structural data at a smaller scale

The annual height increment from 2002 to 2004 was in median 75cm (40-100cm were the 1st - 3rd quartiles) calculated by comparing the heights of 76 canopy trees measured in 2004 (using a line to forest bottom, 20cm accuracy) with the height of these trees in 2002 (Seele 2004, 20cm accuracy, but realistic accuracy 1m due to large number of measured trees, Carolin Seele personal communication). Tree species did not differ significantly in the increments (Kruskal-Wallis one way analysis of variance on ranks p=0.5). It seems that the forest keeps on growing up (see also plate 6), however measurement accuracy and the use of data compiled by different persons do not allow a conclusion.

Crown length was measured for 81 trees as the difference between crown top and crown bottom, defined as the height above which 90% of leaves were found (assessed visually). Contact zones between pairs of trees were characterised after Frech et al. (2003) and Frech (2006) by measuring their width (horizontal), height (vertical) and assessing the intensity of contact. The width was defined as the greatest contact distance seen from above (measured with a 5m long stick, accuracy ½ m), the height as the difference between the upper and lower contact points of the crowns (i.e. points in which leaves of the neighbouring trees are adjacent; each measured by a line to forest bottom, accuracy 20cm), and the intensity of contact was classified as: 1. Gap between the crowns greater than 50cm, 2. Crowns touch each other (intermediate between 1 and 3), 3. Crowns go into each other for more than 50cm. Overall 121 contact zones were measured, 86 of which between trees in patch type 2, the equivalent to the forest studied by Frech (2006).

Crown length was in median 8m (range 3-28m, 5-10m were 1st to 3rd quartiles) and made in median ¼ of total tree height (16%-31% were 1st to 3rd quartiles). *A. pseudoplatanus*, *F. excelsior* and *T. cordata* differed significantly from *Carpinus betulus* in crown length (means

± standard deviation: 7.7m ± 3.1m, 6.9m ± 2.9m, 7.2m ±3.1m versus 15.2m ±5.2m respectively, t test $p<0.001$). This is a clear instance of dimorphism in tree height (as defined in the model of Iwasa et al. 1984, being the only one describing a mixture of height strategies – Falster and Westoby 2003). Moreover, a minimal thickness (of ca. 3m) exists, as implicated in equation 11 of Iwasa et al. 1984, in contrast to frequently used models that take the crown to be "infinitely thin" (Gratzer et al. 2004). Crown length of trees included in patches of type 1 (see above) was significantly smaller than crown length of trees included in patches of type 2 or 3 (mean crown thickness ± standard deviation were 6.0m ± 2.6m, 8.6m ± 3.2m and 9.2m ± 5.7m respectively, t test $p=0.012$ for types 1 vs. 3, and $p=0.001$ for types 1 vs. 2).

The modal contact zone was 2-3 meter wide, 3-4 meter high. The height of the contact zone was 5-15% of the tree height (64% of the cases, 94% are up to 20%). The width and height of the measured contact zones are significantly correlated (Pearson product moment coefficient 0.35, $p=0.0002$), their regression was: Width of contact zone = 2.6m + 0.38 · Height of contact zone (slope and constant $p<0.001$). The width of the contact zones differed significantly between patch types 1 and 2 and types 1 and 3, but not between types 2 and 3 (Mann-Whitney rank sum test $p = 0.04$, $p<0.001$ and $p=0.12$ respectively). The height of the contact zones did not differ significantly between patch types (Kruskal-Wallis one way analysis of variance on ranks $p=0.24$). Most contact zones begin in the 20-24m layer and end in the 24-28m layer (above the dead wood zone, see below).

Pairs of tree species (interspecific and intraspecific) were checked for differences in the contact zones between them (as a comparative study to Frech 2006). Differences in height and width of the contact zones were not statistically significant taking all measured contact zones (Kruskal-Wallis one way analysis of variance on ranks $p=0.5$ for width, $p=0.9$ for height of contact zones, no two species pairs differed significantly, Mann-Whitney rank sum test all $p>0.08$). Neither were significant differences in the intensity of interaction among the different pairs (all had median 2 except one pair with 3; first quartiles of all were 2 except one pair with 1, the third quartile of half of the pairs was 2, of the other half 3).

Taking only contact zones in patch type 2 (a similar forest stage as in Frech 2006), contact zones of *Carpinus betulus* with *T. cordata* and with some *A. pseudoplatanus* were longer than in other pairs. The measurements were too few to reveal the differences among interacting pairs, and the work of Frech (2006) is recommended as a thorough treatment of the subject.

Tree species seemed to differ in contact zone characteristics in respect to their twig morphology (plate 1, the terms club and whip were suggested by Skip van Bloem):

1. *F. excelsior* has thick and straight twigs ("clubs") in a relatively low density in the crown, that act mainly to break competing twigs. This results in relatively short interspecific contact zones at the top of the crown (as branches are strongly upwards inclined) with a gap between interacting trees. Such contacts are also found between parts of crown of different main branches and seem to be an important factor shaping mature crown form. *A. pseudoplatanus* has twigs of a similar type.
2. *C. betulus* and *T. cordata* (as well as *Prunus avium*) have long thin and flexible twigs ("whips") in a high density that tend to tangle into each other, resulting in longer contact zones with smaller gaps and sometimes interlaced branches of neighbouring trees. Interactions of trees of different types result in clearing of the "whips" by the "clubs" (typical to *F. excelsior – T. cordata* interactions), "creeping" of "whips" below the "clubs", as the thicker branches are less moveable by the wind and thus less destructive (Niklas 1992, typical to *C. betulus - F. excelsior* interactions) or whipping off the "clubs" (observed on small *F. excelsior* near larger *Prunus avium*, plate 1).

Thick and thin branches also differ in the intensity of mechanical competition they inflict. Thicker branches usually move with a smaller amplitude (except when they are very long) but inflict more damage on bordering twigs than thinner branches. This difference can be directly observed on the distances between branches and twigs, but was not quantified. It comes to an extreme in small canopy trees growing very close to large canopy tree, whose upper, still relatively thin main branches are broken yearly by thick branches of the larger tree.

All contact zones studied clearly resulted from mechanical abrasion by neighbouring trees (or main branches within the tree), as evidenced on scars on the branches and observation of the stand on windy days. It seems that most damage was done when the trees are bare of leaves – thus lighter and more easily moved by wind than when they are loaded with foliage that increase their mass and impact but also their inertia. This study thus supports the observations on "crown shyness" (Roloff 2004) in other forests (Rebertus 1988 and references there) and deems this term rather inappropriate. The tree crowns are in no way shy, they are involved in a severe battle for space. As shown in the main part of the study, crown area was the crucial parameter in respect to flowering intensity and fruit set, and determine so the few most reproducing trees (figures 6, 16b, 31a, 34c, tables 17, 27). Branch types may well be responsible for the species-specific crown form as mechanical abrasion was observed also

between main branches of individual trees as well. It may be possible to model the typical sways in terms of the vertical distribution of branch thickness at different branch orders and the related elasticity modules (Niklas 1992).

Dead wood was assessed on 22 trees of different species and sizes in vertical layers 4m thick starting from the forest floor upwards (uniformly for all trees). Twigs and branches were categorised after their diameter (up to 5cm with 1cm accuracy, thicker with 2cm accuracy) and their length was measured with a 5m long stick (accuracy ½m). Diameters of twigs and branches were measured by a conspicuously tagged ruler tied to the end of the stick, unreachable branched were assessed visually in comparison to reachable branches.

Dead wood was most frequent at the upper half of the trees (12-24m) and was scarcely found at stem space and in the upper crown. In particular, most dead wood was located below the contact zones. Thin twigs (<2cm) had their center of distribution at 16-20m, lower than middle thick and thick branches (together ≥3cm, centered at 20-24m height). This difference reflects large branch systems, especially in *F. excelsior*, that bent downwards and died of other reasons than mechanical abrasion). The vertical distribution of dead wood thus depends on its property, or dimension, that is studied - the main volume (and mass) of dead wood is concentrated higher than the main length of twigs, whereas the surface of dead wood is distributed quite evenly on a wider range than both. Organisms utilising different aspects of dead wood (e.g. fungi that colonize the surface, Unterseher 2006, versus insects that burrow inside the wood, Schmidt 2004) may have different height distributions according to the distribution of their "interpretation" of the substrate.

The different locations of leaf mass, flowers and fruit, contact zones (mechanical competition) and dead wood within the crown highlight the many functions, and thus the many interpretations, that a tree crown may have (Bongers 2001). Coarsely stated, upper crown is responsible for assimilation and flowering, whereas lower crown (and dead wood! e.g. in *F. excelsior*) is responsible for sustaining the space needed for further growth. Reality is of course more complex, as vegetative and reproductive processes control the speed of growth, which determines the ability to mechanically compete with neighbors. For example – shoot growth in the terminally flowering *A. pseudoplatanus* becomes sympodial and weaker than the original monopodial growth, so that reproduction weakens the ability to mechanical competition (Sakai 1990, Roloff 2004, see also plate 6)).

Climate

Local climate and flowering phenology

The climatic data for the study periods were received from Germany's national weather service (Deutscher Wetterdienst, DWD) for the station Leipzig airport (figure 43). Additionally, data from this station from the last 33 years were analysed in order to appreciate the probabilities of climatic events that seemed to influence the flowering of the studied species, especially of *F. excelsior*.

The temperature sum curves ($(T_{max}+T_{min}) / 2$, start of summing on 1.1 each year, Cenci et al. 1997), from middle March on, were for 2003-2005 quite similar (the curves are within a range of 100° in every Julian day from each other) whereas they were lower than the curve for 2002 in 100-150°C. These years are within the normal range since 1973 (1979, 1985-7 and 1996 were exceptionally cold, ca.200°C below the normal range). The end of winter as the last minima of the curves differed however much between study years (middle January for 2002, second half of February in 2003 and first half of March for 2004 and 2005, corresponding to table 29).

DWD starting dates for *F. excelsior* from the station Leipzig North are in average 25 days later than the starting dates found here (differ significantly in a t-test, $p<0.001$), and for the study years do not even have the same order (Spearman rank order coefficient $p=1$). The DWD dates represent a temperature sum for the starting of flowering that is 300°C higher than the starting dates here (404°C versus 106°C), and neither of the starting dates correlated significantly with the temperature sums in different years (Pearson product moment, $p=0.2$ and 0.9).

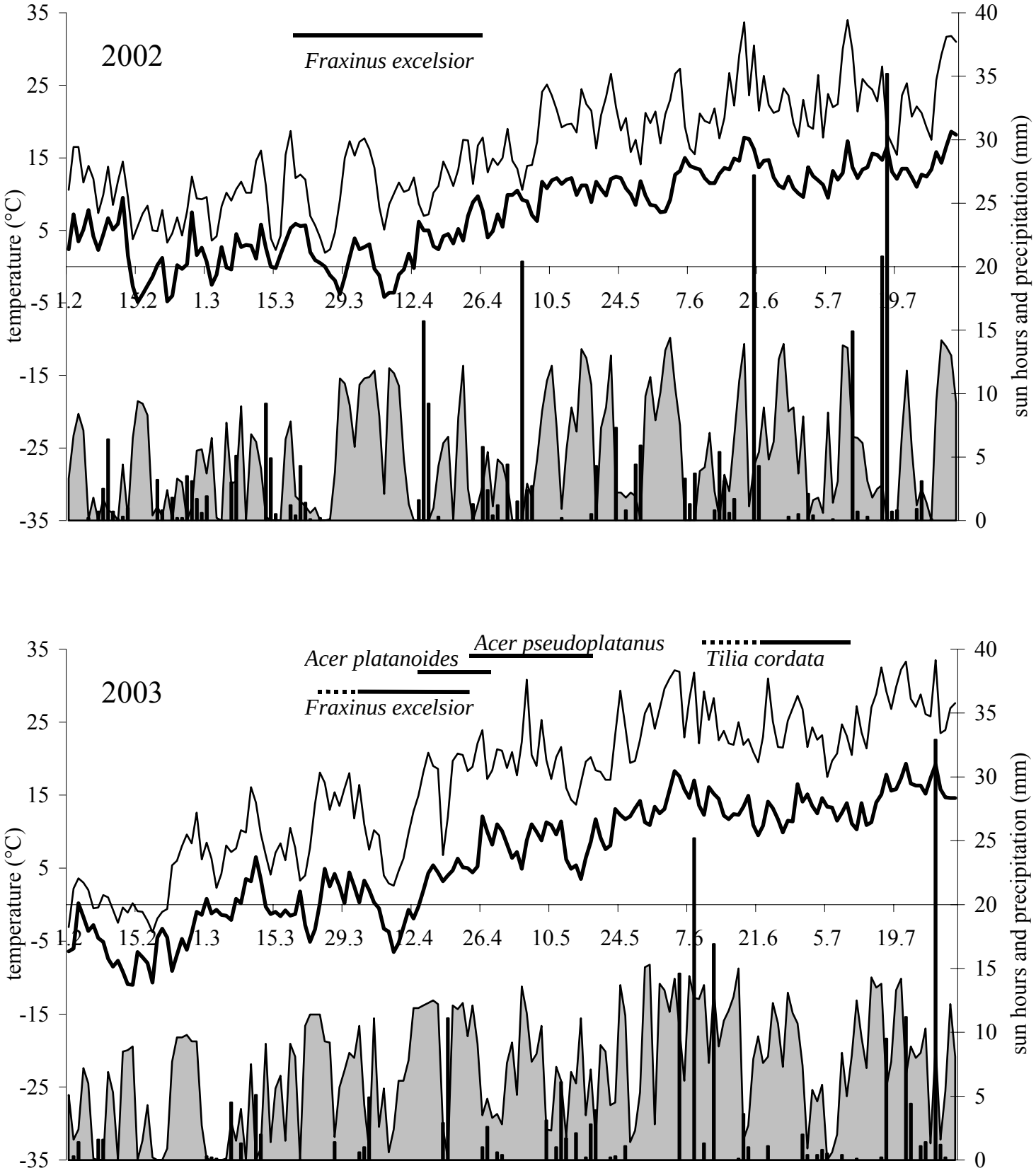
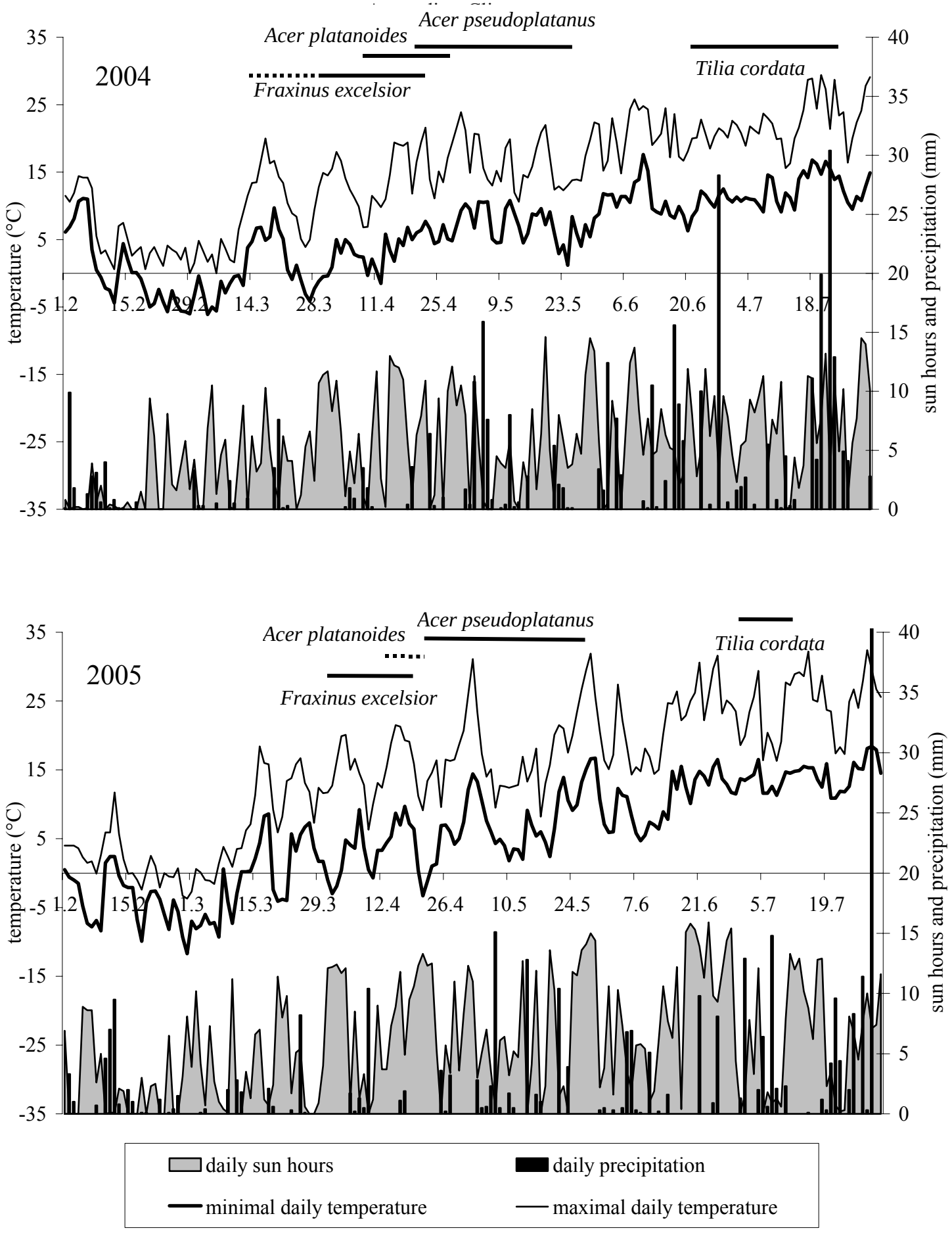


Figure 43: Climatic data for February to July in the study years. Minimal and maximal daily temperature as lines, daily sun hours shaded grey, and precipitation as black balks. The bars above each diagram indicate the flowering periods of the studied species, broken lines indicate flowering of one or two trees only.


2004
Acer platanoides
Acer pseudoplatanus
Fraxinus excelsior
Tilia cordata
temperature (°C)
sun hours and precipitation (mm)
35
25
15
5
-5
-15
-25
-35
40
35
30
25
20
15
10
5
0
1.2
15.2
29.2
14.3
28.3
11.4
25.4
9.5
23.5
6.6
20.6
4.7
18.7
2005
Acer platanoides
Acer pseudoplatanus
Fraxinus excelsior
Tilia cordata
temperature (°C)
sun hours and precipitation (mm)
1.2
15.2
1.3
15.3
29.3
12.4
26.4
10.5
24.5
7.6
21.6
5.7
19.7
daily sun hours
daily precipitation
minimal daily temperature
maximal daily temperature

The species flowered sequentially from March to July, from early spring to the summer. Different aspects of the weather affect the flowering in different ways:

1. Temperature: Frost damage (figure 14b, plate 4) and temperature effects on flowering phenology in *F. excelsior* (see below), little frost damage to *A. platanoides*, and a general effect of temperature on the speed of inflorescence unfolding and flower development (figure 14, plates 3,4 and 6, Norby et al. 2003). Sufficient warmth is necessary for successful pollen tube growth and may limit fruit set in *T. cordata* (Pigott and Huntley 1981), but not in *A. pseudoplatanus* (Pigott and Warr 1989).
2. Rain: Drizzle washes pollen from the air (McDonald 1962, Whitehead 1983, Niklas 1985, Crane 1986) and soaks inflorescences (especially the dense inflorescences of male *F. excelsior*, but these lengthen to dry out, plate 4, Tal 2003). Strong rains may damage and wash out flowers (Latorre and Bianchi 1998) and early terminate male anthesis (Whitehead 1983, Tal 2003).
3. Sun: Initiates male flowering in *F. excelsior* (figure 14c, plate 3, Niklas 1985).

These factors also affect pollinator abundance and efficiency by regulating their activity (Corbet 1990, Unwin and Corbet 1991, Corbet et al. 1993).

The flowering phenology of *F. excelsior* seems to depend on two main factors – the end of the last long cold period ("end of winter") and intermediate cold periods after flowering has begun ("cold interruptions"). The long period of flowering in 2002 seems to relate to an early beginning due to an early end of winter and to the lack of a clear change in weather (table 29). In 2004 and 2005 as a contrast, the end of winter was late and marked, and was followed by a clearly distinguishable period of warmth (second half of March), these corresponded to a short and intensive flowering period. Sun and rain for themselves seemed to play a smaller role in deciding the beginning and ending of flowering, and their effects are more noticeable on a smaller scale – initiation of male anthesis in the inflorescences (figure 14c, plate 3) and washing out inflorescences respectively.

Table 29: A qualitative interpretation of the climate diagrams (figure 43) in relation to *F. excelsior* flowering phenology.

year	end of winter[1]	anthesis lengthened? - cold interruptions[2]?	start flowering at beginning of warm period - which?	start flowering at a sunny period?	end of flowering at a rain period?
2002	before February	much - 2	yes - ±2nd	no	no
2003	end of February	medium - 1	no (only one tree yes - ±3rd)	no	partial
2004	middle March	no – 0 (with first tree: medium – 1)	yes - 2nd (one tree 1st)	yes (1st tree not)	yes
2005	middle March	no - 0	yes - 3rd	yes	no

[1] Last period of 10 days with minimal temperature below -1°C.

[2] 5 days in a row of minimal daily temperature below +1°C.

The crucial parameter is the timing of temperature changes and not the temperatures themselves (similar to the conclusions of Schemske et al. 1978 and species differences in this aspect in Ahlgren 1957). As an illustration, the accumulation of heat sum was equal from the beginning of March to middle April in study years (5.3±0.3°C/day in all study years) but the patterns of flowering phenology differed much.

The flowering duration of the anemophilous *F. excelsior* was more variable than that of the other, entomophilous, species, in accordance with the results of Bolmgren et al. (2003) and different than Rabinowitz et al. (1981). The yearly variance however underlines the importance of long term studies and understanding different, species specific physiological reactions to climatic factors (Körner in press).

The flowering phenology of *Acer* spp. and *T. cordata* does not seem to clearly coincide with climatic events (except for the first phase in *A. pseudoplatanus* in warm or sunny periods), and the study of them for two years only does not permit conclusions. The climatic data do not seem to supply clear cues to flowering as in the case of *F. excelsior*. In face of the high synchrony that was found in *Acer* spp. (table 12), and its low sensitivity to gross temperature

manipulation (Norby et al. 2003), the cue may be sought in a different factor (day length? Taiz and Zeiger 2000, Lehrbuch der Botanik für Hochschulen 2002). The effect of rain washing out pollen is similar, and the effect of sun initiating flowering was also observed in these species (figure 31b, plate 6), but in a much more limited scope than in *F. excelsior*.

The analysis of DWD data in 1973-2005 yielded the following frequencies of climatic events:

1. Cold periods (end of winter): The proportion of cold periods (of ten days in a row with minimal daily temperature below –1°C) decreases from 50% at the first half of February to 20% at the beginning of March and is zero by the beginning of April. Less stringent cold periods (seven days in a row with minimal temperature below +1°C) appear a frequency of 20% in February, become more common (30%) in the second half of March and then decrease in frequency to 10% in the first half and 2% in the second half of April.
2. Cold periods (cold interruptions and frost in April): The proportion of years with one "cold interruption" in April (separate periods of at least five days in a row with minimal temperature below +1°C) was 25% (two interruption happened only in one of the years). In 60% of the years April had 6-10 frost days (minimal temperature below 0°C), in 12% 11-15 and in 23% 0-5 frost days.
3. Rain events: The probability for light rain (1mm per day) is quite constant from March to July (1,2,3,5 days in a row - 100%, 90%, 60%, 20% per month respectively). In contrast, the probability for a day with heavier rain (10mm) increases constantly from 40% in March to 80% in July.
4. Sunny periods: The probability for periods of sunny days increases from March to Mai and then remains constant until July (e.g. a week with more than four daily sun hours happened in 20% of the years in March, 40% in April and 70-80% in May to July, the probability for a four days period with six daily sun hours at least increases from 40% in March to 80% in April to July).

This analysis shows that in *F. excelsior*'s flowering time the probabilities for cold interruptions and damaging frost events during flowering are still high, and the probability for a long sunny period also increases during flowering time. However, the probability for a strong rain is relatively low in early spring, which may be advantageous to this wind pollinated species (the probability for weak rains is quite constant during the spring).

Microclimate in the forest

Vegetation cover has a great influence on the microclimate at its surrounding (Stoutjesdijk and Barkman 1992) and the forest canopy is prominent in these effects, but as tree crowns are rather difficult to reach, data are rather scarce (see for temperate forests Heckert 1959, Wilmers and Ellenberg 1986, Stoutjesdijk and Barkman 1992, Geiger et al. 1995 and for tropical forests Madigosky 2004 for references).

A microclimatic study was pursued between March 2004 and September 2005, in which differences in temperature and humidity within the forest at scales from 100m (edge effects), 10m (vertical dimension), 1m (effects of crown envelope) and 1-10cm (local effects of branches, twigs, inflorescences, leaves) were measured in respect to seasonal changes, especially to the unfolding of leaves and to the flowering phenology of the studied species (Ehleringer 1989).

The measurement instruments (plate 1) were:

1. A hobo® (ONS-H08-032-08, www.synotech.de) measuring temperature and relative humidity (vapour pressure deficiency was calculated after the formula in Corbet and Unwin 2005). Temperature measurement is crude, due to the large thermal mass of the sensor. Measurement accuracy was taken as 1°C (producer's accuracy of 0.4°C at 23°C plus assessed differences between sensors and temporal reading error) and 5% relative humidity (producer's accuracy 3%). The hobos® were covered by a white plant pot to be shaded and to protect the humidity sensor from getting wet.
2. A hobo® data-logger (ONS-H08-008-04) connected to four N thermistors (ONS-27-9M1002-C3) in form of black beads or pinheads 2mm across. The sensors were soldered to the logger cables after the manufacturer's scheme (Wolfgang Vocke, personal communication) and protected from moisture using a drop of transparent epoxide resin glue. Measurement accuracy was taken as 1°C (producer's accuracy of 0.5°C at 20°C).

The sensors were placed to measure the following differences (more data in Tal et al. in press):

1. Vertical in the forest. Hobos® were placed at upper and lower crown and in lower stem region, and the measured differences were analysed in respect to their vertical

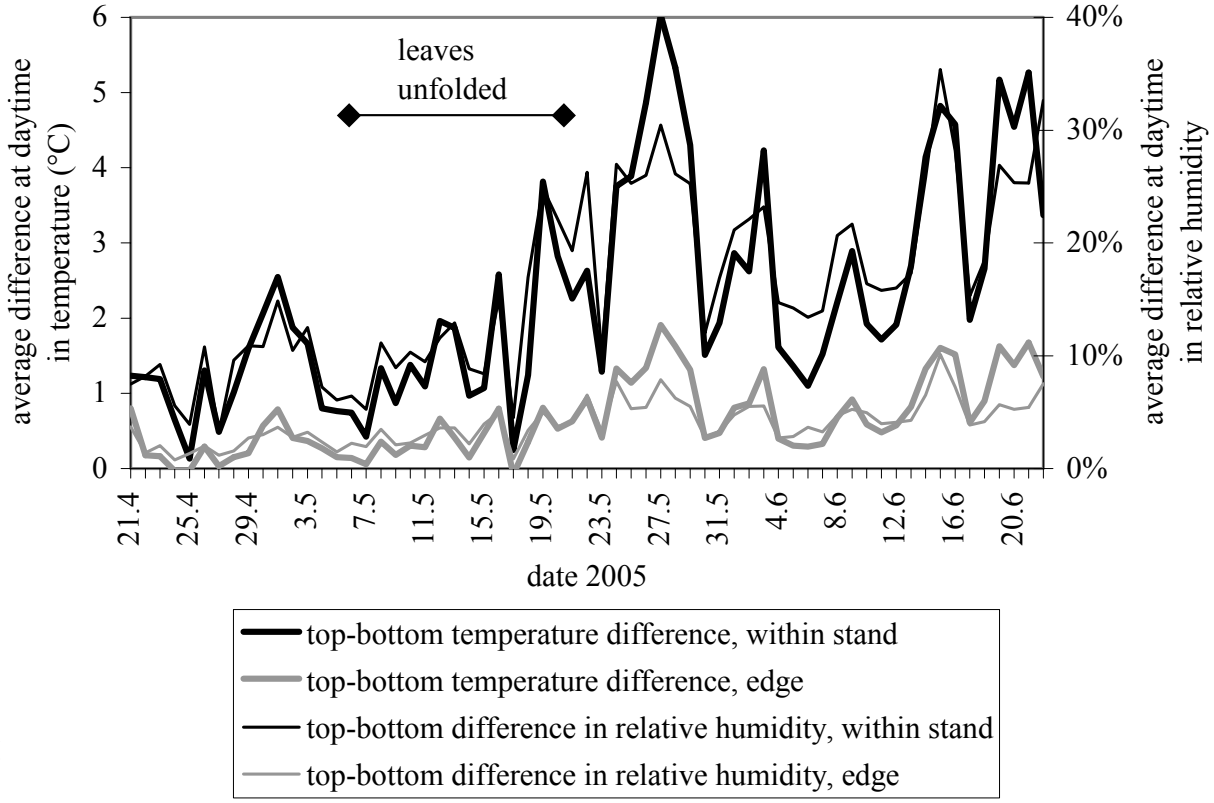
partitioning. The vertical gradient was compared between a location within the forest and a location at the forest edge as well as before and after leaves unfolded. The average deviation of the measurements from the measurements of Stephan Bonn (Dresden university, department of forest sciences) in the study site at a comparable location in the crown for 8.4-27.6.2004 was smaller than my measurement accuracy.

2. Horizontal across the crown envelope. Black beads (thermistors) were placed across the crown envelope (outside, within and inside) and were either expose or shaded by leaves.
3. Local differences. Beads were placed on different aspects of branches, twigs and leaves, and within paper bag covers that manipulated flowering phenology.

The main findings for the flowering period (April to June) were (see details in Tal et al. in press):

1. Vertical differences (figure 44a): Before leaves unfolded only minor large-scale differences were found. After foliage appeared a marked gradient was measured, crown top being warmer and drier than forest bottom at daytime (daily maximum of 7.7°C, 46% relative humidity and 17mbar vapour pressure deficiency). This difference was much larger inside the forest than on its edge. The vertical gradient across the crown was larger than across the stem space, especially in temperature. During the night and during rain events the vertical differences disappeared. Temperature and humidity difference were strongly correlated among themselves and with the number of daily sun hours.
2. Horizontal differences (figure 44b) were marked after leaves unfolded, the outer crown being warmer than inner crown and sunlit locations warmer than shaded ones. However, the differences were variable during the days and in one case a sun fleck was indicated by a shaded sensor being warmer than a nearby sunlit one (less than 1m long, lasting about an hour). The results underline the variability induced by sun movement and crown and canopy structure.

a:



b:

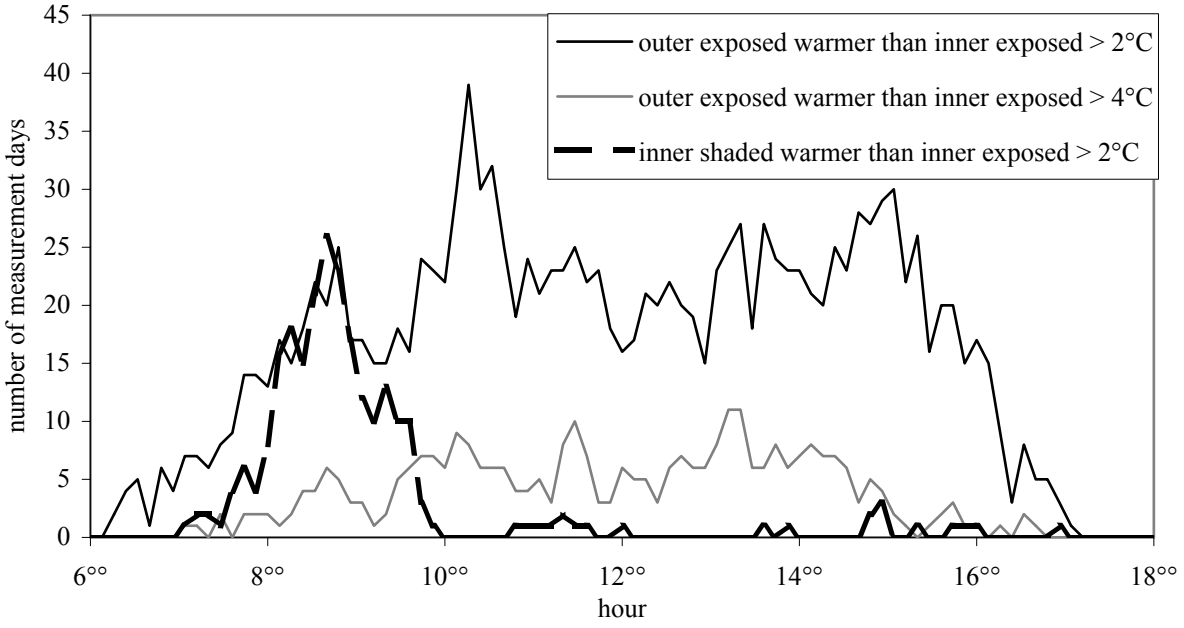


Figure 44: Climatic gradients in the forest. **a**: Vertical gradient in temperature and relative humidity and its temporal and spatial emergence. The average differences during daytime (8°°-18°°) between top (ca. 30m) and bottom (ca. 5m) sensors are shown at two locations ca. 70 m apart, during the spring (leaves unfolded 6-21.5.05). **b**: Horizontal gradient in temperature across the crown envelope of a *T. cordata*. The number of measurement days (of total 86) in which the outer exposed and/or the inner shaded sensors were warmer than the inner exposed sensor, after the hour in the day (24.6-27.9.04).

3. Local differences (figure 45a) were in some cases large. Before leaves unfolded, the 1-10cm scale was the main scale on which the microclimatic variability in the forest was found. Differences up to 9°C were found between two sides of *F. excelsior* twigs, that were significantly correlated with the number of daily sun hours (see also Unterseher and Tal 2006 for branches and Nicolai 1986 for trunks). After leaves unfolded difference persisted but were much smaller. Covering twigs with paper bags induced a large temperature difference, inducing an accelerated phenology that was used as an experimental manipulation *in vivo* (figure 14b, plate 4).
4. All temperature and humidity differences were correlated with the surrounding climate – daily sun hours and daily minimal and maximal temperature. This means that the measured differences can actually be extrapolated according to the regression coefficients to these parameters. In other words microclimatic differentiation is highly predictable in terms of daily sun hours and structural parameters (surrounding canopy structure and local crown structure, see also Hutchison and Matt 1977 for irradiance distribution), and thus may be used to simulate microclimate in this and other temperate broad-leaved forests.

Leaf unfolding is a major event in early spring that affects the microclimate of the forest (Stoutjesdijk and Barkman 1992, Geiger et al. 1995, Tal et al. in press and see below). Its major effects are:

1. Establishment of a temperature and humidity gradient at daytime (upper canopy warmer and drier than lower crown and stem space, figure 44a).
2. Inhibition of wind below the canopy (Wilmers and Ellenberg 1986, Geiger et al. 1995, Nathan and Katul 2005) and impediment of wind pollination.
3. Protection from rain and sun, at least potentially.
4. A major physiological change in the trees, attraction of herbivores that may damage flowers as well (Wellings and Dixon 1987, Teulon et al. 1998, Leather 2000) and insects attracted to them (potential pollinators and parasitoids, Thomas and Blanford 2003), as well as a reduction of showiness of flowers.

The direct effect of climate was most clear and most versatile on *F. excelsior* (figure 14, table 29, plates 3 and 4). Very few effects were observed for the other species (figure 31b, plates

5,6 and 7). Experimental manipulation of microclimate of the inflorescences had results only in *F. excelsior* (figures 14 and 45b, plate 4).

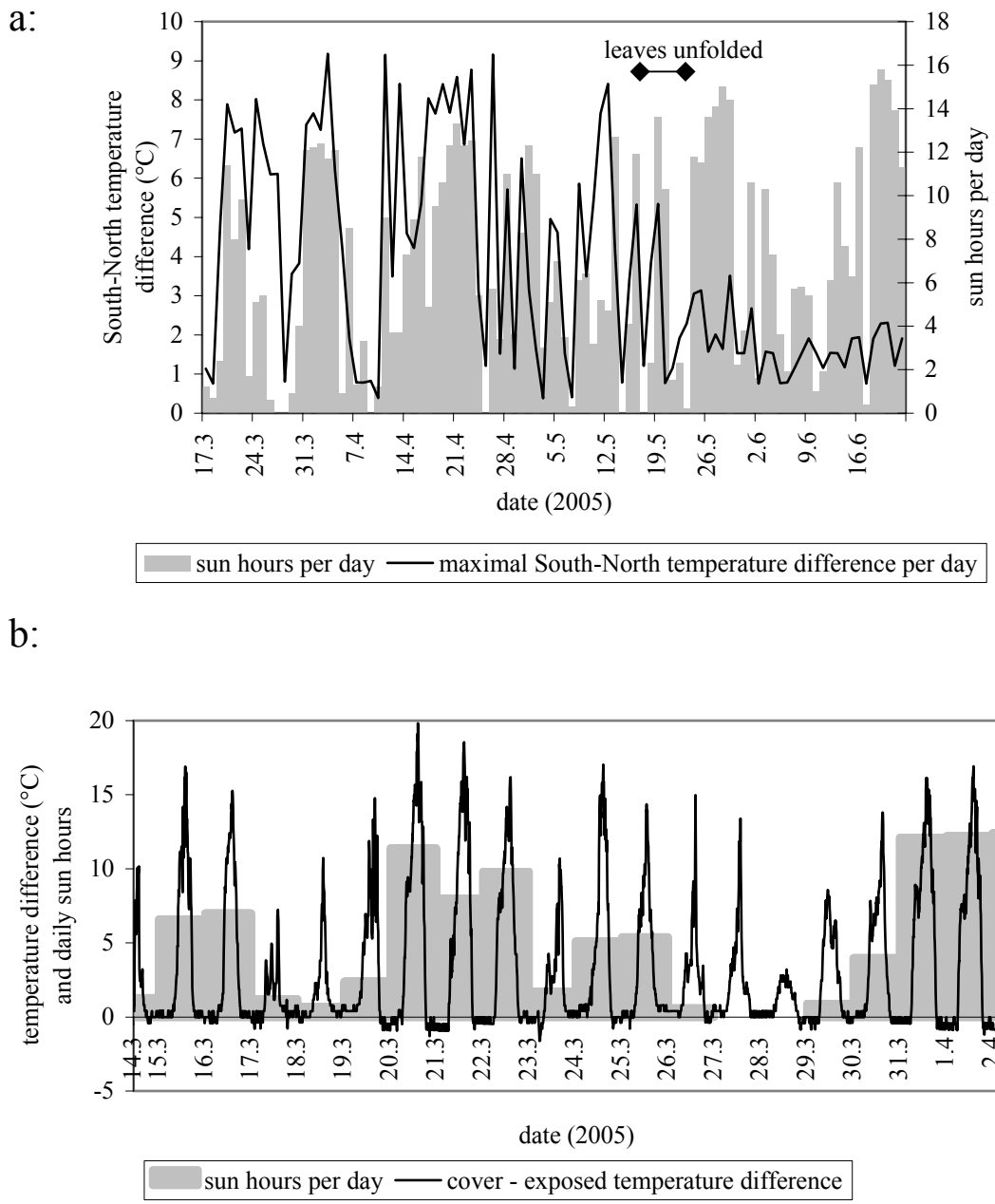


Figure 45: Temperature differences around twigs of *F. excelsior*. **a**: Maximal daily temperature excess (line) of the sensor on the southern aspect of a 1cm thick twig relative to the sensor on its northern aspect, and number of daily sun hours (columns). Measurement period is 17.3-22.6.05, including the period in which the leaves on this tree unfolded - 18-21.5.05. **b**: Manipulation of inflorescence temperature. Temperature difference between a covered and an exposed inflorescence during two weeks in early spring (line) and daily sun hours.

Genetic variability of *F. excelsior*

The genetic variability of populations of *F. excelsior* in Europe is studied in the framework of the Fraxigen project (www.fraxigen.net, Aldinger et al. 2001, Heuertz et al. 2001, Morand et al. 2002, Petit et al. 2003, Bacles et al. 2005). The detailed reproductive data in this stand and the large variability that was found among the trees may enable an individual based comparison of phenotypical and genetic variabilities, which has not been done before. In addition, canopy access enabled a sampling of the trees that may reveal somatic differentiation within the trees, a controversial factor that may be important to the maintainance of variability in long living trees (Whitham and Slobodchikoff 1981, Antolin and Strobeck 1985, Klekowski et al. 1985, Klekowski. and Godfrey 1989, Gill et al. 1995 but see Orive 2001). For example, the interpretation of the effects geitonogamy in relation to pollination mode and to flowering phenological patterns in the crown, is very different depending on the resulting variability of the seeds.

All studied *F. excelsior* were sampled, as well as smaller trees and saplings in the stand. Overall 454 leaf probes were taken from 95 trees in the stand, nine saplings and 20 trees outside the stand or of other *Fraxinus* spp., almost every tree was sampled from at least two different main branches, 14 trees were sampled at ten or more points differing in the distance along branches between them. AFLP and microsatelite sequences were analysed for the sampled and their variability is assessed (see Parolin et al. in press for methods and references).

Results of an initial sampling separate males from hermaphrodites and females and reveal a very high variability among as well as within trees.

Plates

The following plates illustrate the main findings. My poor photographic skills limited the usefulness of the photos as figures in the text but I hope that together with the legends they may convey the findings more vividly. Most of the photos were improved with Photoshop® (mainly lighting conditions and color ranges) and scales are not presented as they were in most cases not exactly measured during photography, but they are annotated when relevant.

The plates illustrate in turn the themes:

1. The plot, structure and instruments.
2. Flowers of *Fraxinus excelsior* and *Acer pseudoplatanus*.
3. *Fraxinus excelsior* inflorescences.
4. *Fraxinus excelsior* - microclimatic effects on inflorescence phenology.
5. *Acer pseudoplatanus* inflorescences.
6. *Acer platanoides*.
7. *Tilia cordata*.
8. Arthropods and the inflorescences of the studied species.

Plate 1: The plot, structure and instruments

1. A view of a part of the plot around the rail at the time of flowering of *F. excelsior* before leaves unfold.
2. An aerial photo of LAK's plot with crowns of most canopy trees outlined in black and classified to patches outlined in different colors for different types (see table 26).
3. Instances of mechanical competition between trees:
Up – A part of the contact zone between two *F. excelsior*. The twigs in the front belong to different, neighbouring trees (note the corresponding left and right hand twigs in the background). The photo illustrates the "club" form of competition. Both twigs have scars and are somewhat eroded as they clash by the movement of the trees, swaying in the wind (Niklas 1992).
Down, left – A contact between a branch of *Prunus avium* (coming in from the left), of the "whip" type of branch, and a lower *F. excelsior* (middle of photo). The intensive contact is evident on the broken tips of *F. excelsior* branches (note the growth of lateral twigs instead of the broken apical shoot) and the shiny appearance of the bark of the *P. avium* branch on its lower side.
Down, right – A closer look at one of the *F. excelsior* twigs from the middle photo, with foliage. The broken apical shoot is seen on the lower part of the photo and the lower part of the new shoot is deformed and eroded.
4. Microclimate sensors. Left - A "black bid" sensor (thermistor, 2mm in diameter) embedded in a drop of epoxide resin glue (shiny and transparent) for protection against moisture connected (over a resistance) to a cable leading to the data logger. Right – A hobo® measuring temperature and relative humidity attached to a branch and covered with a plant pot for protection against direct irradiance and rain.
5. Up - *T. cordata* twigs covered with a paper bag (left) and with a 0.2mm mesh size net (right). A third cover used was a 1mm mesh size net (not shown on the photo). Down – A bird net stretched between an *F. excelsior* (left) and a *Populus* x *canadensis* (right) using canes attached to their branches and cable ties to tighten the net to them. The net on the photo is 6m long and 2.5m high, shorter nets of 2m and 3m were used between neighbouring trees and within tree crowns.

Plate 2: Flowers of *Fraxinus excelsior* and *Acer pseudoplatanus*.

(1-8). *F: excelsior.* Flower forms – male (1), balanced hermaphrodite (2) and female-biased hermaphrodite and female (3). The right hermaphrodite flower and the left female flower are at the same scale to illustrate the size the stigma of female (or female-biased hermaphrodite) flowers can reach when not pollinated. The stigmas are compared more closely in (5) – to the left a stigma of a male-biased hermaphrodite and to the right a stigma of a female-biased hermaphrodite, slightly squashed to demonstrate its fleshy consistence. The row in (3) illustrates the variability of anther residues on female-biased hermaphrodite flowers, which may coexist within one inflorescence and partly depends on the location of the flower in the inflorescence and on microclimate. (4) tries to present the variability of anther form and size – male flowers have rhombic anthers (ca. 2mmx2mm, up) whereas anthers of balanced hermaphrodite flowers are pointed at their end and somewhat smaller. The lowest photo demonstrates the variability within an hermaphrodite inflorescence. (6) presents male and female flower forms on an exceptional tree. These male and female flowers are mixed at inflorescence level and differ in form and color from flowers on other *F. excelsior* trees. This tree also had especially heavy seeds, buds that do not spread open but fall as a cap and had on two years no fruit although it flowered intensively. Its contingency to two *F. pennsylvanica* raises the possibility of genetic influence that will be checked (Parolin et al. in press). (7) presents the change of color and surface of the stigmas that was taken to indicate the onset of receptivity after peroxidase test failed (false positives, Tal 2003). Stigmas in balanced hermaphrodite inflorescences were more often observed in a non-receptive state than stigmas in female-biased inflorescences. (8) is a fluorescence microphoto of a group of adjacent germinating pollen grains on a stigma (pollen grain diameter ca. 25µ).

(9). Hydrated pollen grains of the four studied species are presented to the same scale (1mm on the ruler represents 2.5µ, in this way the pollen diameters was measured using Photoshop®, better photos are available at http://paldat.botanik.univie.ac.at).

(10-13). *A. pseudoplatanus* – (10) The flowering phenology of female flowers was recorded using the grade of spreading of the stigma lobes (see table 3). (11) presents male flowers with lengthened filaments before and after anther dehiscence (in nature vertical). A group of adjacent germinating pollen grains is presented in (12). The pollen tubes enter the stigma between papillas. (13) demonstrates young carpels in an embryonic male flower on the male tree.

Plate 3: *Fraxinus excelsior* inflorescences.

1. Male inflorescences. Bud opening (1), waiting phase (2,4) in which inflorescences are completely unfolded but anthers do not dehisce, and the inflorescences persist as a "purple knob", about 2cm in diameter, for up to two weeks. Anthesis proceeds then in the twig as a unit from southern to northern aspect (3). Notice the fine differences in the yellow parts in anthesis in relation to the inclination of the individual twigs (south is at the left of 3).
2. Mainly male and male-biased hermaphrodite inflorescences may present only a few stigmas above the "purple knob" (left), or may develop to extended hermaphrodite inflorescences (right) depending on the location in the crown and on the twig (Tal 2003), on the specific year and probably also on climatic influences.
3. Hermaphrodite inflorescences usually expose non-receptive stigmas at the beginning of inflorescence unfolding (left, lower inflorescence, 1-1½ cm long), these then become lighter in color and receptive as the inflorescence lengthens (2cm, plate 2(7)). Notice the differences in anther sizes between the two inflorescences on the same twig. Apical flowers are exposed first and the basal flower anthesise not until the inflorescence fully spreads (right, to a smaller scale, 3-4cm long).
4. Female-biased hermaphrodite inflorescences usually expose receptive stigmas from their very emergence from the inflorescence bud (left). Basal flowers are exposed gradually as the inflorescence lengthens (right), stigmas of the apical flowers are at the end of receptivity, basal flowers can sustain further receptivity due to the lack of pollen shedded from the apical flowers. Note that the twig is the basic unit of flowering, similar to the male twigs, as all its inflorescences sweep together the air for pollen and act as one aerodynamic unit (Niklas 1985). In this, *F. excelsior* inflorescences are more similar to *Salix caprea*'s upright inflorescences than to pendulous inflorescences (as classified by Kugler 1970, Proctor et al. 1996).
5. Opening inflorescences of different gender in approximately the same scale. Male buds (5) are wider than female buds ((1), ca. 1cm vs. ½cm) and more rounded. The female inflorescence is elongated (2) and keeps on lengthening whereas the male inflorescence is spherical (6) and usually stays in its form until the end of anthesis. The middle inflorescences are intermediate – the female-biased hermaphrodite inflorescence (3) is wider than the female one but more slender than the male-biased inflorescence (4), balanced hermaphrodite inflorescence are quiet similar). Note the few stigmas extruding above the anthers.

Plate 4: *Fraxinus excelsior* - microclimatic effects on inflorescence phenology.

1. Frost damage to male inflorescences. Left: Large damage to lengthened inflorescences, all anthers destroyed, glossy anthers soaked with rain. Middle: Medium damage of slightly unfolded inflorescences (up) and no damage to not lengthened inflorescences (down). Right: Lengthened inflorescences dry out after rain and enable efficient pollen release from late dehiscising lower inflorescences (no frost damage).
2. Frost damage to female and hermaphrodite inflorescences. Left: Large damage, destruction of most flowers in the inflorescence, but note undamaged basal flowers emerging. Right: Medium damage in the inflorescence to the left (note that the apical flowers are more severely damaged) and light damage in the inflorescence to the right.
3. Effects of paper covers on flowering phenology: Left: A comparison of a covered twig (paper bag removed) and an uncovered twig. (1) is on a hermaphrodite tree, covered twig to the left – the inflorescences are longer, the stigmas are of lighter color and frost damage is larger, uncovered inflorescences to the right - less unfolded and stigmas darker but little damaged (figure 14b). (2) is on a male tree, covered twigs to the right – inflorescences somewhat lengthened, after full anthesis (in the background many covered twigs), exposed twigs to the left – inflorescences in the "waiting" phase, not lengthened and before anthesis. Right: (3) shows a cover on a female-biased hermaphrodite, left longer than above and without a frost period (in 2005). The effects of the covering are similar to the left photo – inflorescences longer, stigmas brighter and long in anthesis. (4) – Covers on twigs of female-biased hermaphrodites – The yellow spots on the lower part of the paper bags are pollen shed from these inflorescences. The inflorescences can be seen through the bags to be more lengthened than the surrounding exposed inflorescences.

Plate 5: *Acer pseudoplatanus* inflorescences.

1. Protandrous inflorescences. Left - Inflorescence in the middle of its first male phase (large inflorescences reach 15cm length and 4cm width), note that no differences in anthesis can be seen between the left, sunlit side (south) and the right, shaded side (north), in contrast to the marked differences in *F. excelsior* (plate 3) and *A. platanoides* (plate 6). The gender of unopened flowers cannot be clearly discerned. Middle – the female phase with many stigmas during full anthesis. Gaps along the inflorescence axis represent fallen male flowers of the first phase (some rests are visible at the lower third of the inflorescence). Right - An infructescence. All fruit result from a single flowering phase, although a clear gap along the infructescence axis can be seen. Note the green color of the young fruit, and also that most fruit (e.g. all lower fruit) are flat and devoid of seed.
2. Protogynous inflorescences. Left - The first female phase nearing its end, as evident on the long spread stigma lobes. Stamens of male flowers are not yet lengthened. Middle – The first male phase almost at full extent. The young fruit are seen above in their typically smaller number and grouping at the upper part of the inflorescences, in contrast to protandrous infructescences. Right – The second male phase of flowering. First phase male flowers fell and left gaps along the inflorescence axis, young male flowers are unfolding (e.g. right above the bottom of the inflorescence). This phase is smeared in time (see figure 24).
3. The third flowering phase. (1) and (2) show an exceptional second female phase (third phase of flowering) in protogynous inflorescences. Left - The young fruit from the first phase are in the upper part of the inflorescence, the gap in the middle corresponds to the wilt and fallen flowers of the male phase (some rests are still seen in the lower part of the inflorescence), and female flowers at anthesis are seen at the bottom of the inflorescence (marked with arrows). Right - An infructescence with two sizes of young fruit from two different female phases (rests of the intermediate male phase can be seen among the lower fruit). (3) shows a second male phase in a protandrous inflorescence with few flowers, after a female phase with many flowers. The missing spaces along the inflorescence axis correspond to the wilt and fallen male flowers of the first phase. (4) is a male inflorescence at its last, third flowering phase (compare to figure 37). The large gaps along the inflorescence axis were left by the former two flowering phases, note that some flowers of the current phase are still unfolding. The third phase in all inflorescence types was of small extent (figure 22) and on the male tree in 2005 included a few female flowers.

Plate 6: *Acer platanoides*.

1. Flower gender and measurement of inflorescence length. Left - A female flower at the beginning of anthesis and a male flower at the end of anthesis, a rare coincidence. Stigma lobes lengthen during anthesis and protrude above the closing petals (middle, the maximal stigma height differed between trees). Right - Inflorescence length was measured from basis to furthest point to the next ½ cm.
2. Climatic effects on phenology – Left - The first flowers to come to anthesis lean to the south (right in the photo) in opening inflorescences. Right - Light frost damage in opening inflorescences in mid April. No severe frost damages were observed. Aphid damage, however, was total in 2005.
3. Anther movements during the anthesis of male flowers. Stamens are spread radially at the opening of male flowers and then lean inwards one after the other and dehiscise. Then they either spread out (rightmost photo) or stay curved inwards (photo 1 left). These movements are not ubiquitous but may contribute to exact location of pollen on a bee's head, in the same place in which it would touch the stigma, and to pollen partitioning.
4. Within-crown vitality differences. This photo is of a part of the crown of one large tree. The left part includes long shoots and is of high vitality (Roloff 2001, vitality level 0). Its inflorescence density was lower and its flowering phenology was later in respect to the main crown in the right hand of the photo (vitality level 2). The former crown part represents a reiteration from a main branch which was broken, and may introduce a "juvelinisation" of the tree.

Plate 7: *Tilia cordata*.

1. Overview. An inflorescence with three wilt gall flowers (left) a male flower with a very small pistil rudiment (middle) and a hermaphrodite flower (right, corolla diameter almost 1½cm), both after male anthesis.
2. Bud opening stages (at a common scale) – from left to right – closed, swollen, opening bud, opened flower (male), see figure 31b.
3. Stigma beginning to opening (left), and with fully spread lobes (middle). To the right a flower at the end of female anthesis – petals turned yellow and withered.
4. Male flowers with pistil rudiments of different sizes. In the two flowers to the left they seem nibbled off, in the flowers to the right they seem to be arrested early in development. Anthers in all flower types are bithecate and small, and only about a half of them open. Closed and opened anthers are distinguished by the light yellow color of the former, in contrast to the darker yellow color of the latter.
5. Gall flowers are smaller, petals usually do not fully unfold, stamens degenerated to different grades, flowers open early.
6. Hermaphrodite flowers with a short and thin style were found occasionally, these styles are presented in their final size (2-3mm versus 5mm in normal hermaphrodite flowers, note petals) and did not elongate any more. This flower form is the closest to the one described in *T. japonica* by Ito and Kikuzawa (1999). Below left is such a style in a younger stage - ca. 1mm long and stigma lobes not yet spread.
7. Hermaphrodite flowers with a damaged pistil – on the left photo in the flower to the right the style is clearly curved to the side (arrow), probably a result of sticking to other flower parts in the bud (adjacent a male flower). These flowers usually do not turn into fruit, but exceptions can be found (photo to the right).
8. Inflorescences. (1) - The largest inflorescence found, with 41 flower buds (figure 30c). (2) - The typical pattern of flowering along a twig – the terminal inflorescence is the last to flower (in the photo still all buds closed whereas more basal inflorescence with mostly opened flowers). (3) – Inflorescences usually contain flowers at different stages: A bud, hermaphrodite flowers at the beginning and at the end of female anthesis (white and yellow respectively) as well as male flowers at the end or after anthesis.

Plate 8: Arthropods and the inflorescences of the studied species.

Fraxinus excelsior – Gall mite galls (*Aceria fraxinivorum*). Left – Young galls (1,2) at flower base as swellings (with rests of stamens), commonly scaly or hairy, of pink color, sometimes accompanied by distorted pistils (3). Plant tissue creates many small hairy pockets (4), in which both gall mites (probably 5) and predatory mites (6, in reality about twice as large as the gall mite) can be found (Castagnoli 1996, Sabelis 1996). The gall "pedicels" lengthen (7) and the whole "gall stand" (spangle gall) becomes lignified at a similar timing to the development of infructescences on female trees. Resulting "pedicels" length differs much among trees (8,9). The resulting galls are of large mass on male trees (8,9) whereas single galls at most are found on fruit producing trees (10), often with a fruit wing attached.
Acer platanoides – Insects on flowers – Left - The probably main pollinator – *Andrena* cf. *haemorrhoa* with long visiting times. Middle – a bumblebee – *Bombus* sp., here *B.* cf. *lapidarius* (*B.* cf. *terrestris* were also commonly observed). Right – a nitidulid beetle, *Epuraea melanocephala* escapes from a flower a few seconds after shaking it. Note the inwards bent stamen (see also plate 6). These beetles are also common in *A. pseudoplatanus* and brown, probably second generation beetles are common on *T. cordata*. *Taeniothrips inconsequens* (see below) are also found on *A. platanoides* as adults.
Acer pseudoplatanus – Left - Thrips *Taeniothrips inconsequens* is suspected as the main pollinator. Due to adult activity it may pollinate protogynous trees more effectively than protandrous trees. Inflorescences of *A. pseudoplatanus* are their main reproductive site as only there larvae were found (adults are also found earlier on *F. excelsior* and *A. platanoides*). All but a few adults caught were female. Middle – Aphid larvae caused large damage to flowers, mainly to male flowers in 2005 (results, before table 10). Right – Ants were observed feeding on nectar towards the end of flowering (here cf. *Lasius* sp.). They also cut small holes in paper bags that covered inflorescences on *A. pseudoplatanus* and *T. cordata*.
Tilia cordata - Gall midges (cf. *Dasineura tiliae*) cause flower galls (plate 7). They were frequently observed ovipositing, but as they were small and very quick, this blurred photo (left) is the best one I got (the small spot above and to the left of the bud is the gall midge). In the middle a female gall midge at x20 magnification, the bar represents 1mm. To the right, a true bug *Orius minutus* predates on a *Thrips major* in a male flower.

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Ophir Tal, Leipzig den 22.6.06

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